UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

METHOD OF ESTIMATING FISH POPULATIONS, WITH APPLICATION TO PACIFIC SARDINE

By T. M. Widrig

FISHERY BULLETIN 94

From Fishery Bulletin of the Fish and Wildlife Service

VOLUME 56

UNITED STATES GOVERNMENT PRINTING OFFICE • WASHINGTON : 1954

For sale by the Superintendent of Documents, U. S. Government Printing Office, Washington 25, D. C.
Price 30 cents

CONTENTS

	Page
Theory of the method	141
Introduction	141
General statement of the method	141
Development of the method	142
A hypothetical example	143
Assumptions of the method	144
Satisfying the assumptions	144
Computing an initial-population index	146
Effect of changing availability on total-mortality estimates	146
Estimating availability and total mortality	148
Some hypothetical examples with less than full availability	149
Summary	154
The method applied to the sardine fishery	154
Source of data	154
Application and results	157
Population size assuming constant availability	158
Population size assuming constant natural-mortality rate	160
Summary	161
Notation	163
Appendix	163
Literature cited	165

METHOD OF ESTIMATING FISH POPULATIONS WITH APPLICATION TO PACIFIC SARDINE

By T. M. WIDRIG, *Statistician*

THEORY OF THE METHOD

INTRODUCTION

One of the most pressing and perplexing problems of fishery biology is that of securing reliable estimates of population sizes. Apart from complete counts of fish, which are impractical for marine species, the tag-and-recapture method of estimating the fraction of the population that is caught in a period of time by a fishery is one that has been commonly practiced on large populations (see Ricker 1948 and Schaefer 1951, for example). This method is both difficult and expensive, as is the one based on annual egg censuses and information on fecundity.

DeLury (1947) has suggested a method of estimating population size using catch and effort data. An assumption necessary to his method is that there be no natural mortality. When catch data are measured over long periods, as annually, natural mortality conceivably could be large with respect to fishing mortality.

The method of estimating population size described in this paper is an elaboration of the method developed by Silliman (1943). It requires data on the age composition of the catch and on fishing effort. The necessary assumptions are more easily satisfied than those required by DeLury (1947).

Since methods of estimating population sizes are difficult and since the estimates are subject to error (the magnitude of which it is often impossible to assess), it is desirable that, whenever possible, two independent methods be used.

GENERAL STATEMENT OF THE METHOD

In attempting to estimate the size of a population, the fishery worker generally knows, first of all, the size of the catch from that population. The problem might then be stated: *What is the ratio between this catch which I observe and the total stock from which it came*? I wish to compute the ratio between the catch and the size of the population from which it came by subtracting the natural mortality rate from the total mortality rate to get the fishing mortality rate. The latter, of course, is the ratio of the catch to the initial stock.

The rate of total mortality can be computed from estimates of the ratio of the stock size in one year to the size of that stock in the following year. For this purpose, information on the age composition of the total catch per unit-of-effort is usually sufficient.

Having computed the total-mortality rate from the catch data, all that remains is to find the natural-mortality rate, so that it can be subtracted from the total-mortality rate to give the rate of fishing mortality.

Under certain conditions, the rate of natural mortality can be derived from two series of data—

1. The number of fishing effort units expended to obtain the given catch.

2. The total annual-mortality rate that the total stock experienced while yielding the given catch.

Briefly, the method of estimating the natural-mortality rate is as follows:

In a fishery that has experienced a wide range of fishing effort between years, and therefore in fishing mortality between years, the total-mortality rate will vary as well. But if natural mortality is constant, a given percentage change in fishing effort should produce a smaller percentage change in total-mortality rate. If natural mortality is large, one expects fishing effort to affect total mortality less than if natural mortality is small.

By examining the past sequence of total-mortality rate and the corresponding fishing effort, one should be able to compute a constant rate of natural mortality necessary to give the observed relation between total mortality and fishing effort.

To examine the relation between fishing effort and the attendant total mortality, I consider a regression of the total-mortality coefficient on the

number of fishing effort units. I show that this relation should be linear, if my assumptions are granted. When fishing effort is extrapolated to zero, the total-mortality rate will be equal to the rate of natural mortality.

DEVELOPMENT OF THE METHOD

If fishing acts so that the catch of a standard unit of gear in a moment of time is proportional to the population size at that moment, then the rate of fishing mortality referred to above will be p (see Notation, p. 163) in

$$\frac{dC}{dt}=pN_t \tag{1}$$

where $\frac{dC}{dt}$ is the rate of catch on time and N_t is population size during time dt. If natural mortality behaves in a similar fashion, that is, q, in

$$\frac{dn}{dt}=qN_t \tag{2}$$

where $\frac{dn}{dt}$ is the rate of natural death on time and q is its coefficient, then the instantaneous rate of total death, say, i, can be expressed as

$$i=p+q \tag{3}$$

Further, under certain assumptions concerning the time and space distribution of p and q, the annual total death rate, expressed as a fraction of the initial population for a unit time period, may be written as a in

$$a=1-e^{-(p+q)} \tag{4}$$

or

$$a=1-e^{-i}$$

since, of course, the total rate of death is the sum of the two rates, when expressed as instantaneous rates. (See Baranov 1918 and Ricker 1940 and 1944, for detailed derivations.) Now u, or the rate of exploitation, can, under certain conditions, be written simply in the above notation as

$$u=p\frac{a}{i} \tag{5}$$

Since a, the seasonal rate of total mortality, often can be estimated from age-composition data, and since i is related to a as

$$a=1-e^{-i}$$

the ratio of a to i is fairly easy to compute from age-catch data. The problem remains to compute p, in order to find u, and hence the population size, given the catch.

Under certain conditions (see appendix, p. 164), fishing effort may be considered as directly proportional to p, say

$$p=Qf \tag{6}$$

where Q is the constant factor of proportionality, and f is number of fishing effort units.

Now only a constant, Q, remains to be estimated, to estimate population size. Recall the relation between Q and the various mortality rates:

$$i=p+q$$

or

$$i=Qf+q$$

If q is constant, and one has measures of i and f, Q will be the slope coefficient in a linear regression of several such relationships, say, one from each season for which data on age-composition and effort are available.

Silliman (1943) solved two similar equations:

$$a_1=m_1+n-nm_1 \tag{7}$$

$$a_2=m_2+n-nm_2$$

where $m=1-e^{-p}$ and $n=1-e^{-q}$ and where

$$\frac{f_1}{f_2}=\frac{\log(1-m_1)}{\log(1-m_2)}. \tag{8}$$

It can be shown that equations 7 and 8 are equivalent to

$$i_1=Qf_1+q \tag{9}$$

$$i_2=Qf_2+q$$

Silliman used sardine total-mortality and effort data that he took to represent an average for two periods of years, 1925–33 and 1937–42. His method is equivalent to fitting a regression line to all his yearly data by the method of semi-averages. The method described in this paper is one of fitting a regression line to all the yearly data by the method of continuous averages, or least squares.

A HYPOTHETICAL EXAMPLE

Suppose that data on the total-annual-mortality rate, a, and effective fishing effort, f, are available for some fishery over a period of several years, as follows (see fig. 1):

TABLE 1.—*Hypothetical mortality and effort data*

	a	f	i		a	f	
		Boat-days				*Boat-days*	
Year 1	0.50	101	0.69	Year 4	0.71	208	1.24
Year 2	.63	153	.99	Year 5	.76	246	1.43
Year 3	.62	161	.97	Year 6	.78	249	1.51

The regression (slope) coefficient is $Q=0.005318$, and the i intercept is $i=0.147$. Thus, with no fishing effort, the data lead one to infer that the total-mortality rate would be $i=0.147$, or 13.7 percent annually. This would be the average natural-mortality rate of the population. And for every 100 boat-days of effort during a season, one would infer that the total-mortality rate would be increased over the natural rate, 0.147, by 0.5318 units. Thus, if there were 100 boat-days in some particular season, one would infer that the fishing-mortality coefficient that those boats generated was $p=0.5318$, and that the total-mortality coefficient during that season was $p+q=0.5318+0.147=0.6788$. This i corresponds to an a of 49.3 percent per year. Of this 49.3 percent, one would infer that the fraction p/i was that part of the initial population that was caught during the season, or $0.5318/0.6788=0.7834$. So, the fraction caught, or rate of exploitation, is 0.7834 times 49.3 percent, or 38.6 percent, with the remainder of total mortality representing the fraction that died naturally, or 10.7 percent. The initial population for that year, of fish that were fully recruited and therefore sustaining these various rates of mortality, would be estimated by dividing the catch for that year by the rate of exploitation, since,

$$u=\frac{C}{N} \tag{10}$$

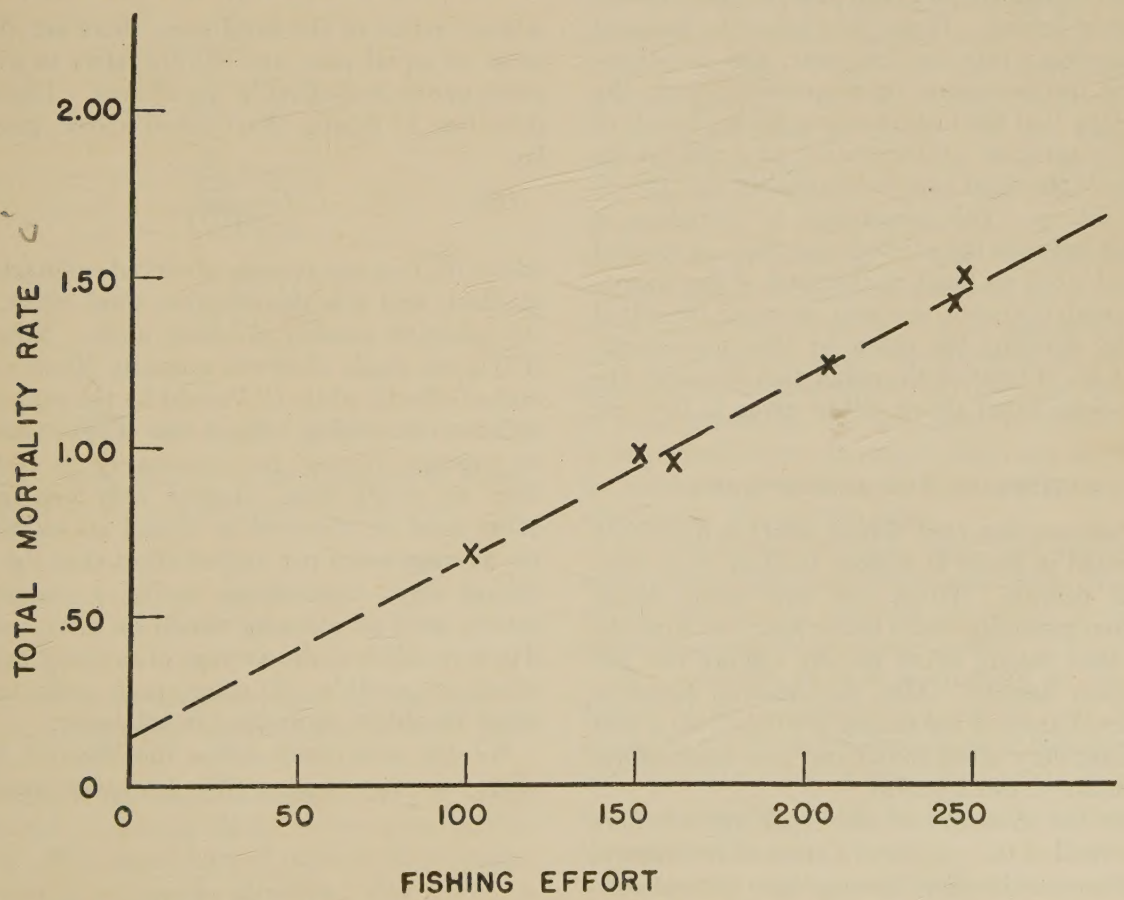

FIGURE 1.—Instantaneous total-mortality rate and fishing effort in an example. Data from table 1 in text.

and therefore

$$N=\frac{C}{u} \tag{11}$$

That is, N, the initial population, would be estimated at 1/.386, or 2.6 times the catch in that season.

ASSUMPTIONS OF THE METHOD

The method, just described, of estimating population size from age-composition data and effort data involves four assumptions, as follows:

1. Fishing effort: Must be equally distributed over the area of the fishery and during the unit time period considered.
2. Natural mortality: Must be either constant or uncorrelated with fishing effort.
3. Fishing efficiency: Effort is directly proportional to p, i. e., Q is constant.
4. Area of the fishery: Encompasses range of the fish.

To summarize, the regression analysis gives the means of computing, for each year, the instantaneous rate of fishing. If one then takes the seasonal total-mortality rate for that year, and its corresponding instantaneous total-mortality rate, the percentage that the instantaneous fishing rate is of the instantaneous total-mortality rate will be the fraction of the total seasonal-mortality rate that is due to fishing. This percentage, by definition, is the ratio between the catch during that season and the total stock on hand at the start of the season. If the catch is known, one may estimate the initial stock by dividing the catch by that percentage.

Methods of treating the catch data to satisfy the assumptions listed above will be given in the next section.

SATISFYING THE ASSUMPTIONS

The assumption that fishing effort is uniformly distributed in space is seldom fulfilled by a commercial fishery. Where fish are more dense, fishermen generally make better catches, with the result that fishing effort usually follows the fish population density. Also, the relative distances of different areas of the fishing grounds from a port of landing very often contribute to a nonuniform distribution of fishing effort.

If one has measures of catch per unit-of-effort from several of the component areas of the fishery, any differences in effort among these several subareas may be easily adjusted to yield an effort and catch per unit-of-effort measure that will not violate the above assumption. A method for doing this has been developed by Beverton and Holt (in press), and is as follows:

Let fishing effort be defined as the ratio between the total catch from an area and the average catch per standard unit-of-effort in that area, for a given interval of time. If one is concerned with the effort measure over several areas, he need only divide the total catch of the several areas by the sum of the average catch per unit-of-effort from the several areas. Since catch per unit-of-effort is really a measure of the relative average population density over a given period of time in a given area, a relative average population size index, $(C/f)_t$, in several given areas over a given period of time would simply be the sum of the average population density in each of the component areas, weighted to the respective area sizes. That is

$$(C/f)_t=\sum_{i=1}^{N}(\overline{C/f})_i \tag{12}$$

where t refers to the total area, there are N subareas of equal size, and $(\overline{C/f})_i$ refers to average catch per unit-of-effort in the i^{th} area. Under the definition of fishing effort given above, generally let

$$f=\frac{C}{(\overline{C/f})} \tag{13}$$

where $(\overline{C/f})$ is the average observed catch per unit-of-effort, and f is the effective total effort, i. e., the effective number of effort units. Note that $(C/f)_i$ is a single observed quantity (from a single unit-of-effort), while C/f would be the ratio of two different quantities. Since the $(\overline{C/f})$ measure is an average, it need not necessarily be observed from an entire fleet. Indeed, only one unit-of-effort need be observed to obtain an estimate of the average catch per unit-of-effort that the total-fishing effort experiences during a season. Of course, such an estimate would be more accurate if it were taken as the average of as many units-of-effort as possible. Further, each such unit-of-effort should be equivalent in efficiency.

We can now easily define the effective fishing effort over any number (N) of areas at once:

$$f_t=\frac{\sum_{i=1}^{N}C_i}{\sum_{i=1}^{N}(\overline{C/f})_i} \tag{14}$$

where f_i is again the effective fishing effort for N areas. This effort measure, f_i, will be one which, if applied uniformly to each area of the fishery, would yield the observed total catch and observed sum of average catch per unit-of-effort.

In other words, this effective effort is a weighted average of the effort in the several subareas, the weights being proportional to the observed average catch per unit-of-effort measure in each subarea as follows:

Let the average catch per unit-of-effort in N areas be

$$(\overline{C/f})=\frac{\sum_{i=1}^{N}(C/f)_i}{N} \tag{15}$$

and recall that

$$C_i=(\overline{C/f})_i f_i \tag{16}$$

Substituting these in (14), we have

$$f_i=\frac{\sum_{i=1}^{N} C_i}{\sum_{i=1}^{N}(\overline{C/f})_i}$$

$$=\frac{\sum_{i=1}^{N}(C/f)_i f_i}{(\overline{C/f})N}$$

$$=\frac{\sum_{i=1}^{N}\left[\frac{(C/f)_i}{(\overline{C/f})}\right]f_i}{N} \tag{17}$$

The ratio $\frac{(C/f)_i}{(\overline{C/f})}$ is the weight factor. Of course, if the population density in each subarea is equal, this weight factor is unity, and in that case,

$$f_i=\frac{\sum_{i=1}^{N} f_i}{N}$$

That is, the total effective effort in that case is simply the arithmetic mean of the effort in each subarea.

Of course, if the effort in each subarea is equal, then the total effective effort is the same as this constant effort, regardless of differences in population density among the subareas. Let $f_i=f'$, a constant.

Then

$$f_i=\frac{\Sigma f_i\frac{(\overline{C/f})_i}{(\overline{C/f})}}{N}$$

$$=\frac{f'\Sigma\frac{(\overline{C/f})_i}{(\overline{C/f})}}{N}$$

$$=f'\frac{\frac{N(\overline{C/f})}{(\overline{C/f})}}{N}$$

$$=f'$$

A practical definition of the necessary subareas, then, is that they be those within which fishing effort is more nearly uniform. Fishing effort between the subareas need not be uniform. In many coastal fisheries, the within-season change in the number of boats fishing from an individual port is not nearly as great as the difference, during the season, between the fleet sizes at the several ports of landing. Where the fishing grounds are near these ports of landing, it would be convenient to define subareas as those that are fished by the fleet operating out of each port of landing.

If the density measure (catch per unit-of-effort) is to be taken as a population measure, then each subarea must be equal in size. Otherwise, the density measures must be weighted by the size of their respective areas, to yield a population estimate. Since the range of operation of units of fishing effort is usually not very variable, the units of gear generally will fish areas of similar size. A careful selection of a unit of effort can sometimes be made such that each unit can be assigned specifically to a certain area.

No treatment of catch data can satisfy the assumption regarding natural mortality. In application, one should consider the effect of various reasonable natural-mortality rates.

The necessity for the assumption on the constancy of the efficiency of a unit of gear can be relieved by a careful measurement of fishing effort, with the objective of the assumption in mind. See the appendix, p. 165 for a detailed definition of this constant.

The fourth assumption is one that can only be directly satisfied by fishing outside the normal

fishing area. The problem of assessing the degree to which this assumption is violated will occupy a major part of this paper.

COMPUTING AN INITIAL-POPULATION INDEX

The catch per unit-of-effort index one usually has from a fishery is an estimate of relative average population size during the time period that the fishing effort has accumulated the observed catch. This period is usually a year or a fishing season.

To compute total-mortality rates, it will be necessary to have an estimate of the initial population, or the population at the beginning of the time unit, rather than the average population being fished, which would occur at some time between the beginning and the end of the season.

If we describe the population at any time, t, as

$$N_t = Ne^{-it} \tag{18}$$

where N is the initial population, and i is a constant rate of instantaneous decrease, then the average population during time t, from 0 to 1, is

$$\overline{N} = N\int_0^1 e^{-it}dt$$

$$= (N)\frac{1-e^{-i}}{i} = (N)\frac{a}{i}, \tag{19}$$

since, if i is constant, the annual or seasonal total-mortality fraction, a, is related to i as

$$a = 1-e^{-i}$$

and the survival fraction s, as

$$s = e^{-i}$$

If we desire an index of initial population, and are given an index of average population (the catch per unit-of-effort index) we may convert the average population to the initial population by multiplying the average population by the ratio i/a.

This has been noted by Ricker (1948) and by Beverton and Holt (in press). The latter authors effect the conversion of average- to initial-population-size estimates simultaneously with an estimate of the rate of exploitation for a series of years, through a process of iteration of a regression equation. Iteration is necessary, since one must have a first estimate of i as derived from some estimate of the survival fraction s. Of course, the only estimate of s one has to begin with is the ratio of average populations in successive seasons of a single year class or group of tagged fish. This first estimate of s enables one to approximate the correction term i/a, and the corrected population-size estimates yield a second and more accurate estimate of s, and so on.

EFFECT OF CHANGING AVAILABILITY ON TOTAL-MORTALITY ESTIMATES

Let a population of fish be those members of a stock of fish that are potentially capable of being fished by a fishery. This population would include fish which in a given season are not within the range of (available to) the fishery, but which are potentially available to the fishery by virtue of the possible movement of the fish into and out of the range of fishing operations, or by movement of fishermen into and out of the range of the population of fish. This population would not be barred by any land barrier from entering the area of fishing and some part of them would be in the area of fishing, while all would be capable of moving in and about the fishing area. Let the ratio of the number of fish in the population that are within the scope of fishing operations during a season to the number of fish in the total population be termed the availability level, or availability (Marr 1951 and Sette 1950).

This definition of availability is somewhat general, but it has real intuitive meaning to any fisherman. Sometimes the fisherman is able, by his scouting, to fish so that most of the population is available to him, but this is not often the case. Most fishing gear is limited to certain depths, areas, or sea conditions, and the population is generally not bounded by these same factors. Thus one often finds that some part of a population is unavailable to a fishery, because of limitations in the physical capacity of the gear to fish the entire habitat or range of the population.

The condition of a population being less than fully available is seldom measured directly. Fishermen's records are of little direct help, since they measure only that portion of the population that is within their range; however, if the availability level were to change, the fishermen's catches of a given year class would immediately change accordingly. The result observed by the fishermen would be an apparent change in the efficiency of a

unit of standard gear. If the physical efficiency of the gear had not changed, an apparent change in the efficiency could only be due to a change in availability. That is, the population range or behavior would have changed relative to the fishery. Such a change is not difficult to observe in catch data, but the absolute level of availability is impossible to compute from catch data alone. Supplementary observations would be required to estimate directly the level of availability of a population to a fishery. This would involve fishing outside the area of the fishery.

Since a fishery yields data only on the fished, or available, population, an estimate of total-survival rate from the fishery would be an estimate of the total-survival rate of the population only if the availability ratio in two adjacent seasons were the same, as follows:

Let N_a be the initial available population. Then the availability level would be r in

$$r=\frac{N_a}{N} \tag{20}$$

Let N_1 be the initial total population in a given year, and N_2 the initial total population in the succeeding year. Then the total-population survival rate would be s, in

$$s=\frac{N_2}{N_1}$$

$$=\frac{\frac{N_{a2}}{r_2}}{\frac{N_{a1}}{r_1}}$$

$$=\frac{N_{a2}}{N_{a1}}\left(\frac{r_1}{r_2}\right)$$

So, if $r_1=r_2$, then

$$s=\frac{N_{a2}}{N_{a1}}$$

That is, if the availability level is constant, this estimate of the total-population survival rate from the fishery is an unbiased estimate of the total-population survival rate, even though the survival rate in the available population may be much lower.

If, on the other hand, $r_1 \neq r_2$, we have

$$s=\left(\frac{r_1}{r_2}\right)\frac{N_{a2}}{N_{a1}} \tag{21}$$

$$=\left(\frac{r_1}{r_2}\right)s^*$$

where s^* is the survival rate computed from the fishery data, N_{a1} and N_{a2}.

Large changes in the availability ratio can render estimates of s^* unreal, if s^* is interpreted as survival rate in the entire population, since survival rate in the unavailable population will nearly always be greater than that in the available population. If all causes of death other than fishing are the same for all fish in the population, survival rate in the available population will always be less than that in the unavailable population, and in the total population. In terms of the total population, this means that the total-mortality rate of the entire population, as a maximum, can be no greater than that of the unfished population, plus that resulting from the fished population being taken entirely each year. The initial stock on the fishing grounds in a given year would then be the survivors of the previous year's unfished population. Of course, the lower the level of availability, the lower is this limit of total-mortality rate of the total population. With availability very low, the population initially on the fishing grounds could be fished out entirely each year, yet in succeeding years the ground could continue to supply fish that annually move onto the fishing grounds from the unfished areas. In this case the total-mortality rate of the fished population would be very high indeed, yet for the total population it could be low.

Closing certain parts of the fishing grounds to fishing has the same effect: No matter how hard the remaining grounds are fished, the total population can suffer only a limited total mortality, depending on the level of availability. (How limited this total mortality will be is influenced, of course, by the ratio of size of the closed area to the total area inhabited by the fish.) This procedure is not as efficient, for fishermen, as the alternative procedure of limiting effective fishing effort so that a desired (for whatever reason) total

mortality of the total population occurs. The effect in this latter instance is to fish a higher average density of fish (catch per unit-of-effort is higher) than in the closed-area procedure, even with the same catch. Limiting the fishing effort is in most cases made practical only by setting a bag limit, and to set a bag limit so that a certain total mortality results, one must have good knowledge of the absolute size of the initial total population each year. Such information about marine fishes is at best extremely rare, but nevertheless important, if the bag limit is used to control total-mortality rate and rate of exploitation.

ESTIMATING AVAILABILITY AND TOTAL MORTALITY

If variation in r is random, an average s^* is an unbiased estimate of s, the total-survival rate. If all mortality but that resulting from fishing is constant, then from a given fishing effort one can compute an "expected," or "normal," survival rate for a population if availability is constant. If availability changes, the observed s^* will depart from the true survival rate accordingly.

A regression of i^*, computed from s^*, on fishing effort, f, will yield a system of s's which would be expected if availability does not change from the average availability of the years to which the regression was fitted. Similarly, Q, or the effort-unit efficiency, computed from the regression, will not be that pertaining to the fished population, but to the total population at the average level of availability. Accordingly, the instantaneous rate of fishing mortality to be expected from a given number of fishing-effort units would be Q times that number of units, and would obtain only if those units fished a population whose availability was the same as the average availability when Q was computed. The efficiency of fishing, then, depends on the level of availability. If availability varies, so will the efficiency of a unit of gear.

It is this variation in the apparent efficiency of a unit of gear that will enable one to estimate the ratio of availability in successive seasons. A rough approximation to availability can be easily obtained by assuming that s', the value of s estimated from the regression, is always equal to s for any year, and then taking the ratio s'/s^* as an estimate of r_1/r_2 for each pair of years for which one has the necessary data. A maximum availability measure can then be computed from the series of r_1/r_2. Of course, this measure of availability is not exact, since s' will seldom be exactly equal to s for a given year. The direction of the change will be different, depending upon whether s was greater or less than s' for a given year.

Although the estimated ratios, r_1/r_2, are not biased, the mean of the resulting availability estimates is a maximum. The s' measures are those pertaining to the condition of average availability over the period of the data to which the regression is applied. If the rate of average natural mortality, estimated from the regression, is at all precise (depending on the extent of variation in availability in the data) one can estimate the survival rate in the available population under the condition of average availability. The relationships between the several mortality rates and availability are as follows:

Let

$$D=D_a+D_u \tag{22}$$

where D is deaths in numbers from all causes, D_a in the available population, and D_u in the unavailable population, so that $S=S_a+S_u$, where S is number of survivors from all causes of death, S_a in the available population, and S_u in the unavailable population. Then $S=N-D$. Now

$$s=\frac{S}{N}$$

$$=\frac{S_a+S_u}{N}$$

$$=\frac{s_aN_a+s_uN_u}{N}$$

So

$$s=s_ar+s_u(1-r) \tag{23}$$

Taking

$$s'=s_a\bar{r}+s_u(1-\bar{r})$$

Then

$$s_a=\frac{s'-s_u(1-\bar{r})}{\bar{r}}$$

If s_a were known, one could interpret the slope, Q_a, of the resulting regression of i_a on f as the efficiency of fishing, and the product, Q_a times f, as p_a.

Then

$$u=\left(\frac{p_a}{i_a}\right)a_a$$

and

$$N_a=\frac{C}{u}$$

Now, s_a is seldom known. But there is another, although less precise, procedure for estimating Q_a, with only s^* and f known.

The general expression for the total-population total-instantaneous-mortality rate, in terms of natural mortality, fishing effort, and the level of availability, can be developed as follows:

$$s=rs_a+(1-r)s_u$$

or

$$\begin{aligned}e^{-i}&=r(e^{-i_a})+(1-r)e^{-q}\\&=r(e^{-Q_af})e^{-q}+(1-r)e^{-q}\\&=e^{-q}[r(e^{-Q_af})+(1-r)]\end{aligned}$$

so that

$$(24)\qquad i=q-\log_e[re^{-Q_af}+(1-r)]$$

Of course, if $r=1.00$, this becomes

$$\begin{aligned}i&=q-\log_e e^{-Q_af}\\&=q+Q_af\end{aligned}$$

as before, since $Q_a=Q$, when $r=1.00$, and $i_a\doteq i$. Also, when $f=0$,

$$\begin{aligned}i&=q-\log_e[re^{-0}+(1-r)]\\&=q-\log_e[1]=q,\text{ as before.}\end{aligned}$$

But for $f>0$, and $r<1.00$, i is less than i_a. Further, when $f=\infty$, i is not ∞, but is limited. That is, i has an asymptote, with respect to f, when $r<1.00$. It is

$$\begin{aligned}i&=q-\log_e[re^{-\infty}+(1-r)]\\&=q-\log_e[1-r]\end{aligned}$$

Thus, the locus of total mortality on effort, with less than full availability, will be curved—the slope decreasing as effort gets larger. The fitted straight line, then, is not entirely without bias, especially for higher effort levels. The true total-mortality curve will be an exponential with negative exponent, as in formula 24, and therefore the higher the effort, the more rapidly the slope decreases. One can substantially reduce this bias by transforming the fitted straight line to a curve of the type of equation 24. One might take an estimate of $\bar{r}$ and $\bar{q}$, to approximate the transformation. The straight line gives a fairly accurate measure of $\bar{r}$ and $\bar{q}$, and by taking the mean i and the mean f as coordinates of a point that is common to both the curve and the fitted straight line, one simply solves equation 24 for Q_a.

$$Q_a=\frac{\log_e\left[\frac{\bar{s}-s_u(1-\bar{r})}{\bar{r}s_u}\right]}{\bar{f}}$$

The population size would be estimated as previously outlined, taking Q_a and q to get u_a and N_a, and taking the estimates obtained above to get r and hence N.

This estimate is not necessarily unbiased or consistent. In an example to follow, where r is variable, it will turn out to be slightly biased.

SOME HYPOTHETICAL EXAMPLES WITH LESS THAN FULL AVAILABILITY

In the foregoing hypothetical example, I assumed that there was full availability—that the entire range of the population was sampled by the commercial fleet. These samples would render possible the easy computation of total-population relative size, and the total-mortality rate of the population. Further, the fishing effort was directed at least to some degree over the entire population.

With less than full availability, only part of the total population is fished and the unavailable remainder suffers only natural mortality. With a migratory-fish population, the magnitude of the fished part can be expected to vary, both with the habits of the fish and of the fishermen that pursue them.

Estimates of total mortality from the fished population alone are far worse than estimates from a regression of total mortality on fishing effort. Even these estimates are not exact, but if availability is constant, they are very close. If availability varies, they depart somewhat from the true total-population total-mortality rate. Estimation of the ratio of pairs of successive-years' availability is fairly accurate, but computing the fished-population size is more difficult. The total-population size, of course, would follow from knowledge of the fished-population size and the corresponding availability level.

Estimation of the mortality rates in the fished population can be accomplished in the manner outlined in the preceding section, but they are not entirely unbiased. Further, their reliability is difficult to ascertain, since one has no assurance that availability is varying at random.

Some hypothetical examples will illustrate the magnitude of variation of i^* from i, for various given conditions of availability. The examples assume fishing effort to be increasing throughout the period of years considered.

Example 1 (see table 2 and fig. 2):

(a) Availability constant at beginning of each year=50 percent.

(b) Natural mortality=0.

The regression of i_a on f is straight, but i on f is curved down; i is always less than i_a, as expected. The limit of i is 0.69, or a=50 percent, of course.

TABLE 2.—*Computation of mortality rates, for given fishing effort, with constant natural-mortality rate, availability level, and fishing-effort-unit efficiency*

Constants $\begin{cases} Q_a=0.01 \\ r=50 \text{ percent} \\ q=0 \end{cases}$

f=fishing effort
p_a=instantaneous fishing-mortality rate=$Q_a f$
i_a=instantaneous total-mortality rate=p_a+q
s_a=survival rate, annual,=e^{-i_a}
s=survival rate, annual, in total population=$rs_a+s_u(1-r)$, where: s_u=survival rate, annual, in unfished population=e^{-q}
i=instantaneous total-mortality rate in total population=$-\log_e(s)$

	f	p_a	i_a	s_a	s	i
Year 1	10	0.1	0.1	0.90	0.95	0.05
Year 2	20	.2	.2	.82	.91	.09
Year 3	30	.3	.3	.74	.87	.13
Year 4	40	.4	.4	.67	.84	.17
Year 5	50	.5	.5	.61	.80	.22
Year 6	60	.6	.6	.55	.77	.26
Year 7	70	.7	.7	.50	.75	.28
Year 8	80	.8	.8	.45	.72	.32
Year 9	90	.9	.9	.41	.70	.35
Year 10	100	1.0	1.0	.37	.68	.38
	∞	∞	∞	0	.50	.69

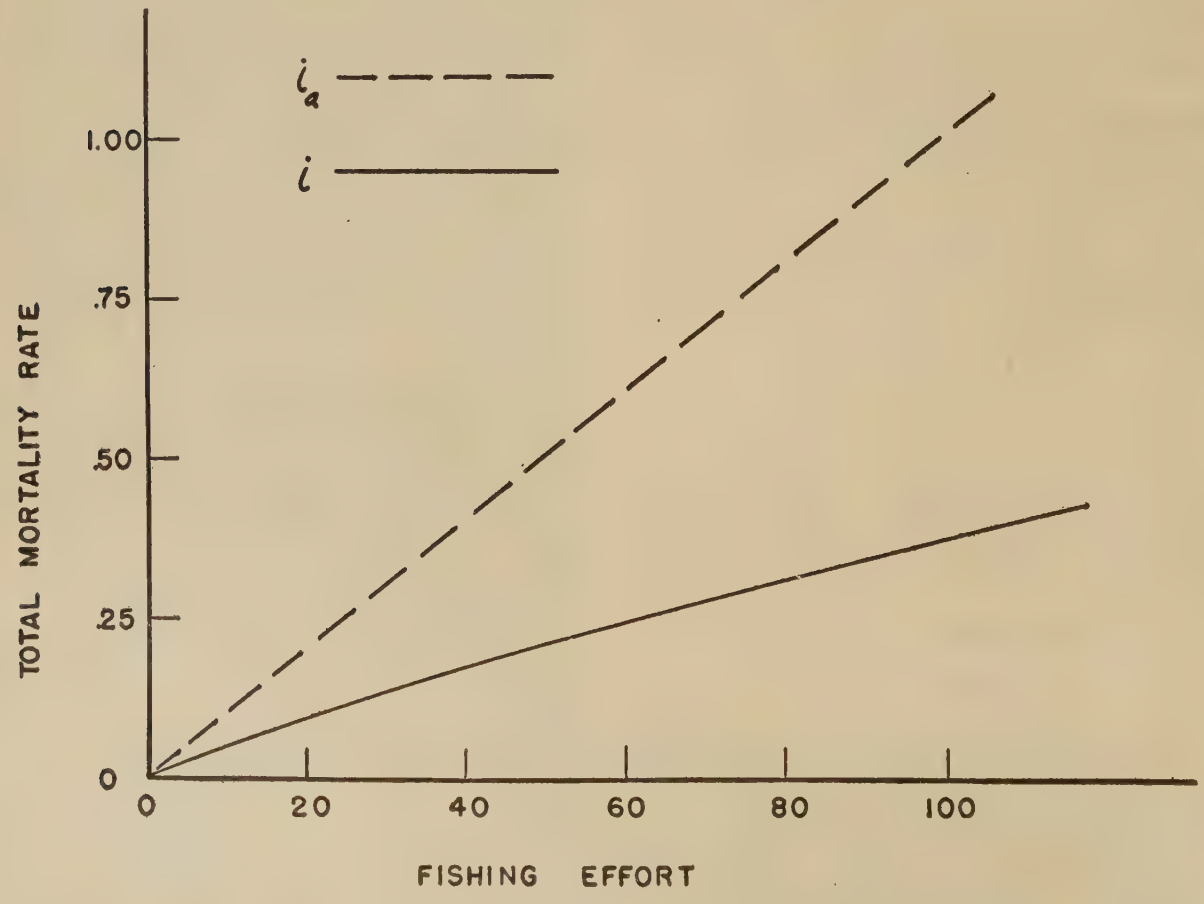

FIGURE 2.—Instantaneous total-mortality rate and effort, from example 1 in text.

Example 2 (see table 3 and fig. 3):

(a) Availability constant at beginning of each year=50 percent.

(b) Natural mortality: $q=0.2$, or $a=18$ percent in unfished population.

Again, i_a on f is straight, while i on f is curved down. Both regressions originate at $i=0.2$, and i is always less than i_a. The limit of i is 0.89, as expected ($=0.69+0.2$), or $a=59$ percent.

TABLE 3.—*Computation of mortality rates, for given fishing effort, with constant natural-mortality rate, availability level, and fishing-effort-unit efficiency*

Constants $\begin{cases} Q_a=0.01 \\ r=50 \text{ percent} \\ q=0.2 \end{cases}$

f=fishing effort
p_a=instantaneous fishing mortality rate=$Q_a f$
i_a=instantaneous total-mortality rate=p_a+q
s_a=survival rate, annual,=e^{-i_a}
s=survival rate, annual, in total population=$rs_a+s_a(1-r)$, where: s_a=survival rate, annual, in unfished population=e^{-q}
i=instantaneous total-mortality rate in total population=$-\log_e(s)$

	f	p_a	i_a	s_a	s	i
Year 1	10	0.1	0.3	0.74	0.78	0.25
Year 2	20	.2	.4	.67	.74	.30
Year 3	30	.3	.5	.61	.71	.34
Year 4	40	.4	.6	.55	.68	.38
Year 5	50	.5	.7	.50	.66	.41
Year 6	60	.6	.8	.45	.63	.46
Year 7	70	.7	.9	.41	.61	.49
Year 8	80	.8	1.0	.37	.59	.53
Year 9	90	.9	1.1	.33	.57	.56
Year 10	100	1.0	1.2	.30	.56	.58
	∞	∞	∞	0	.41	.89

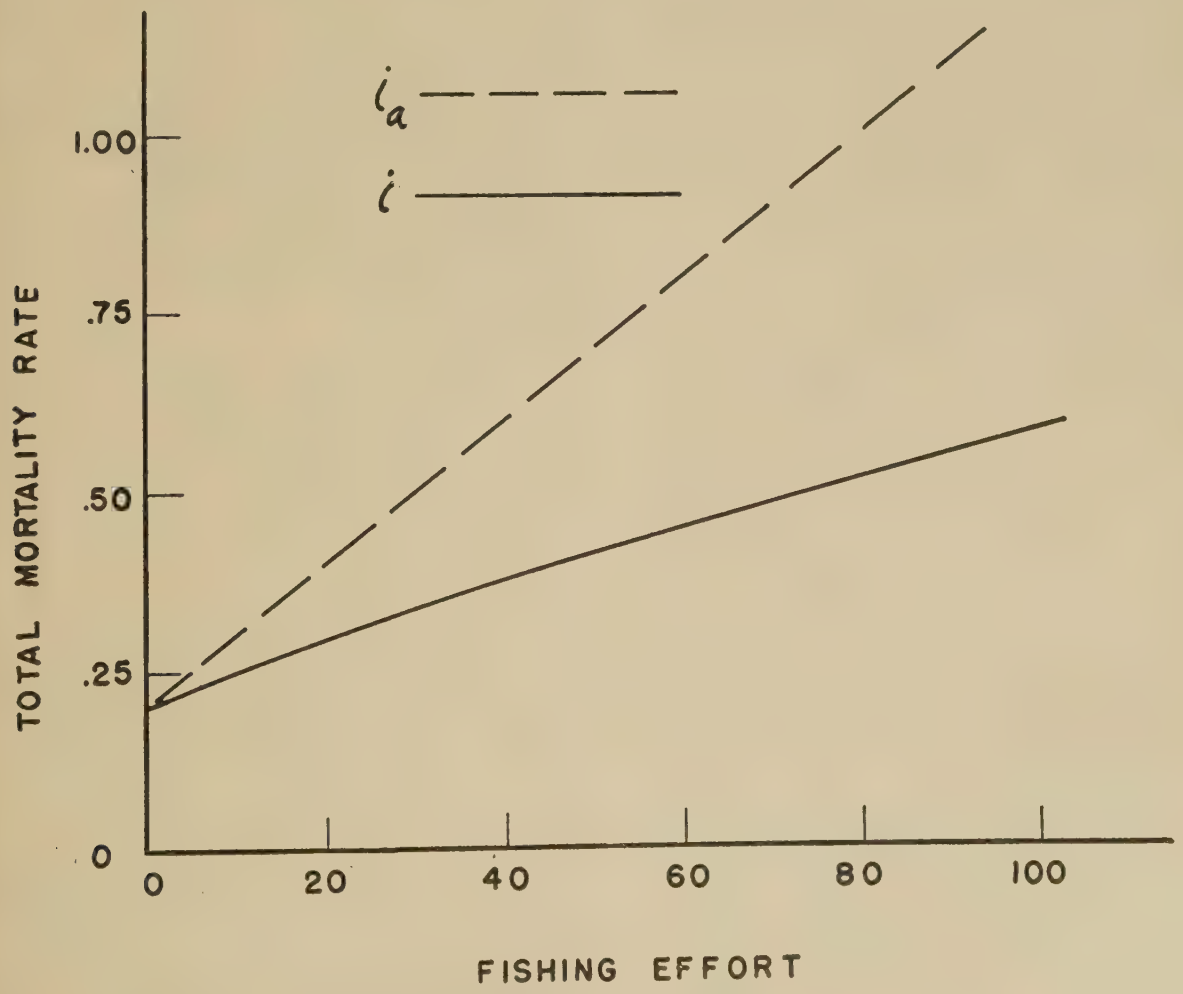

FIGURE 3.—Instantaneous total-mortality rate and effort, from example 2 in text.

Example 3 (see table 4 and fig. 4):

(a) Availability at beginning of each year varying-alternating from 40 to 60 percent in successive years.

(b) No natural mortality.

The limit of a is 50 percent, although it would vary from 60 to 40 percent each year when $f=+\infty$.

In this example I have computed the s^* series: these figures are those that one would obtain if he had only the catch data from which to estimate total mortality. Note that i^* goes from minus values to plus values, while of course i does not. The variation in i is around ± 0.1, but the variation in i^* is around ± 0.5! Note that although the variation in i^* is about five times greater than the variation in i, the regression of i^* on f, even though straight, falls very nearly on what a regression i on f would be. In fact, using i' (the regression of i^* on f) as estimates of i, when processed to yield estimates of r_1/r_2, give rather accurate measures of this ratio.

TABLE 4a.—*Computation of mortality rates for given fishing effort and availability level, with constant natural-mortality rate and fishing-effort-unit efficiency*

Constants $\begin{cases} Q_a=0.01 \\ q=0 \end{cases}$

f=fishing effort
p_a=instantaneous fishing-mortality rate=$Q_a f$
i_a=instantaneous total-mortality rate=p_a+q
s_a=survival rate, annual,=e^{-i_a}
r=availability level
s=survival rate, annual, in total population=$rs_a+s_u(1-r)$, where: $_u$=survival rate, annual, in unfished population=e^{-q}
s^*=available population survival rate, annual,=$s\left(\frac{r_2}{r_1}\right)$
i=instantaneous total-mortality rate in total population=$-\log_e(s)$
i^*=instantaneous total-mortality rate in available population=$-\log_e(s^*)$

	f	p_a	i_a	s_a	r	$1-r$	s	s^*	i	i^*
Year 1	10	0.1	0.1	0.90	40	60	0.960	1.44	0.04	−0.37
Year 2	20	.2	.2	.82	60	40	.892	.59	.12	.53
Year 3	30	.3	.3	.74	40	60	.896	1.34	.11	−.29
Year 4	40	.4	.4	.67	60	40	.802	.54	.22	.61
Year 5	50	.5	.5	.61	40	60	.844	1.27	.17	−.24
Year 6	60	.6	.6	.55	60	40	.730	.49	.31	.71
Year 7	70	.7	.7	.50	40	60	.800	1.20	.22	−.18
Year 8	80	.8	.8	.45	60	40	.670	.45	.40	.80
Year 9	90	.9	.9	.41	40	60	.764	1.15	.27	−.14
Year 10	100	1.0	1.0	.37	60	40	.622	.41	.47	.89

TABLE 4b.—*Estimation of the change in availability level from regression of* i* *on* f

i'=points on regression line corresponding to given f, and assuming q to be zero
s'=estimate of s (from regression)=$e^{-i'}$
$(r_2/r_1)^*$=estimate of $(r_2/r_1)=s^*/s'$
(r_2/r_1)=actual availability level ratio

	i'	s'	$(r_2/r_1)^*$	(r_2/r_1)
Year 1	0.04	0.961		
Year 2	.08	.923	1.50	1.50
Year 3	.13	.878	.64	.67
Year 4	.17	.844	1.53	1.50
Year 5	.21	.811	.64	.67
Year 6	.25	.779	1.57	1.50
Year 7	.30	.741	.63	.67
Year 8	.34	.712	1.62	1.50
Year 9	.38	.684	.63	.67
Year 10	.42	.657	1.68	1.50
			.62	.67

Example 4 (see table 5 and fig. 5):

(a) Availability variable. No regular pattern to the variation in availability. Average availability is 73 percent.

(b) Natural mortality: $q=.2$, or total mortality of 18 percent per year in the unfished population. The limit of total mortality of the total population at average availability is 88 percent per year. Note the wide variation in i^*, while i is much less variable. Table 5a and figure 5 illustrate this situation.

In table 5b the availability ratios and a set of maximum-availability estimates from s^* are computed for comparison with the true availability levels. The true average availability is 73 percent, while the estimated maximum-availability average is 75 percent, in this example. The availability ratios are unbiased (expected to average neither greater nor less than the true average). An example of estimating the availability levels and Q_a is contained in table 5b.

A linear regression of i^* on f yields a q of .245, and a Q of .00511. The true q is .2, and if the mean i is taken as the $\bar{i}^*$, or .526, Q is .00593.

The estimates $q^*=.245$, $\bar{i}^*=.526$, $\bar{r}^*=.75$, and $\bar{f}=55$, yield an estimate of Q_a of .00720. The true Q_a was .01000. Note, however, that the true $q=.2$, $\bar{i}=.513$, $\bar{r}=.73$, and $f=55$, yield a Q_a of only .00800!

The actual i corresponding to a constant r of 73 percent, with $q=.2$, at $f=55$, is $i=.57$. That is, the process of taking $\bar{i}$ and $\bar{f}$ as coordinates of a point on the locus of i with r constant at 73 percent, does not give the exact Q_a that was used with the r not constant, even though its mean was 73 percent. This implies that the procedure of estimating Q_a suggested above is biased. In this example r was fluctuating widely, yet the estimates of it were not far wrong. I have not attempted to get an unbiased estimate of Q_a, but the procedure I chose gave fairly close estimation. In applying these procedures to observational data, then, one should keep in mind that the tolerance of the estimates of such things as $\bar{r}$, Q_a, and q cannot be computed from the theory given in this paper. The accuracy of estimation in the preceding example has been shown to be fairly good, and, in this example, r was varying a great deal. One can expect similar accuracy of estimate in problems where r is varying over a similar range. If there

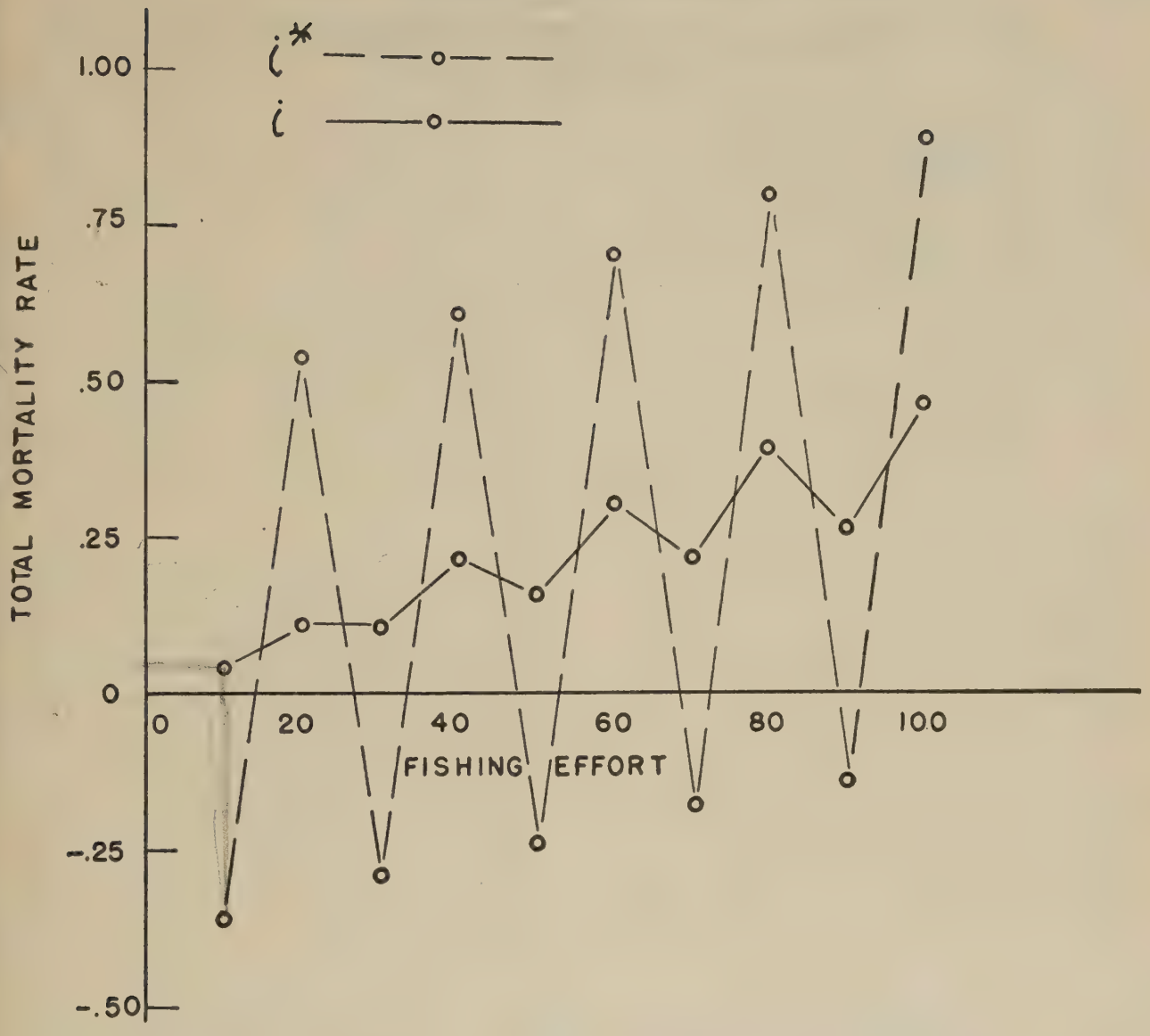

FIGURE 4.—Instantaneous total-mortality rate and effort, from example 3 in text.

is a trend of r on f, the estimation will be less accurate than if r is varying at random with f.

Briefly, with less than full availability the regression of s^* on f will not be linear, but a curve—an exponential with negative exponent—and will have an asymptote (limit). The intercept will, as with full availability, be an average rate of natural mortality. Varying availability will produce extreme variation in s^*, but the locus of average s^* for given effort will yield an unbiased estimate of the average natural-mortality rate, as well as an estimate of the efficiency of a unit of gear as applied to the total population, with average availability.

A first approximation to availability can be obtained from a straight-line regression to the data from which a second and better estimate can be obtained, both of a series of maximum-availability levels and the efficiency (assumed constant) of a unit of gear, on the available population. Knowing this constant, estimates of the size of the available population can easily be computed.

It is only necessary to divide the available population by the availability level, to obtain the total population. Since the availability estimates are maximums, the resulting total population-size estimates are minimums.

TABLE 5a.—*Computation of mortality rates for given fishing effort and availability level, with constant natural-mortality rate and fishing-effort-unit efficiency*

Constants $\begin{cases} Q_a=0.01 \\ q=0.2 \end{cases}$

f=fishing effort
p_a=instantaneous fishing-mortality rate=$Q_a f$
i_a=instantaneous total-mortality rate=p_a+q
s_a=survival rate, annual,=e^{-i_a}
r=availability level
s=survival rate, annual, in total population=$rs_a+s_a(1-r)$, where: s_a=survival rate, annual, in unfished population=e^{-i_a}
s^*=available population survival rate, annual,=$s\left(\frac{r_2}{r_1}\right)$
i=instantaneous total-mortality rate in total population=$-\log_e(s)$
i^*=instantaneous total-mortality rate in available population=$-\log_e(s^*)$

	f	p_a	i_a	s_a	r	$1-r$	s_ar	$s_a(1-r)$	s	s^*	i	i^*
Year 1	10	0.1	0.3	0.74	70	30	0.52	0.25	0.77	0.82	0.26	0.20
Year 2	20	.2	.4	.67	75	25	.50	.20	.70	.75	.36	.29
Year 3	30	.3	.5	.61	80	20	.49	.16	.65	.49	.43	.71
Year 4	40	.4	.6	.55	60	40	.33	.33	.66	.61	.41	.49
Year 5	50	.5	.7	.50	55	45	.28	.37	.65	.59	.43	.53
Year 6	60	.6	.4	.45	50	50	.23	.41	.64	1.02	.45	−.02
Year 7	70	.7	.9	.41	80	20	.33	.16	.49	.49	.71	.71
Year 8	80	.8	1.0	.37	80	20	.30	.16	.46	.35	.78	1.05
Year 9	90	.9	1.1	.33	60	40	.20	.33	.53	.53	.63	.63
Year 10	100	1.0	1.2	.30	60	40	.18	.33	.51	.51	.67	.67

TABLE 5b.—*Estimation of the change in availability level from regression of* i* *on* f

i'=points on regression line corresponding to given f, assuming $q=0.2$
s'=estimate of s (from regression)=$e^{-i'}$
$(r_2/r_1)^*$=estimate of $(r_2/r_1)=s^*/s'$
(r_2/r_1)=actual availability level ratio
r^*=estimation of r, from $(r_2/r_1)^*$. Necessary to assume year of maximum r^* is an r^* of 100 percent (full availability). The several r^*'s are therefore maximal
r=actual r

	i'	s'	$(r_2/r_1)^*$	(r_2/r_1)	r^*	r
Year 1	0.26	0.77	1.06	1.07	78	70
Year 2	.32	.73	1.03	1.07	83	75
Year 3	.38	.68	.72	.75	86	80
Year 4	.44	.64	.95	.92	62	60
Year 5	.50	.61	.97	.91	59	55
Year 6	.56	.57	1.79	1.60	56	50
Year 7	.62	.54	.91	1.00	100	80
Year 8	.67	.51	.69	.75	91	80
Year 9	.73	.48	0.10	1.00	63	60
Year 10	.79	.45	1.13	1.00	69	60
					78	60

SUMMARY

The basis for a method of estimating population size has been developed from four assumptions on the nature of fishing and natural mortality. Those concerning fishing can, if the reporting of catches is sufficiently detailed, be relieved. The assumption that natural mortality is constant is not crucial, since it has been shown that, for the levels of fishing intensity considered, variation in level of natural mortality has little effect on estimates of availability and therefore of population size. One cannot ignore variation in natural mortality, of course, but it is not difficult to explore the consequences of its variation in applied examples.

The extent of the range of fishing effort in the data to which one would apply this method is important. The greater the range, the more accurate will be the population estimates. If the range of effort is small, but at a high level (total mortality high), then one can still apply the method, by assuming several different, though reasonable, rates of natural mortality. This results in a range of population estimates that would be as likely to be true as the assumed natural-mortality rates are likely to be true.

The effect of availability, and how to recognize it, has been developed and illustrated.

THE METHOD APPLIED TO THE SARDINE FISHERY

SOURCE OF DATA

Clark and Daugherty (1950 and 1952) give catch per unit-of-effort data for the three major ports of sardine landings in California. To arrive at a catch per unit-of-effort figure that will represent the total population fished at all three ports, these data must be pooled. Since the fishery of two northern ports, San Francisco and Monterey, occupies an area similar to that of the operation out of the southern port, San Pedro, I have divided the entire fishery into two parts that are approximately equal in area. The catch per unit-of-effort from the two northern ports, then, measure one unit of the population jointly. That is, the catch per unit-of-effort from either of the northern California fleets should measure the relative

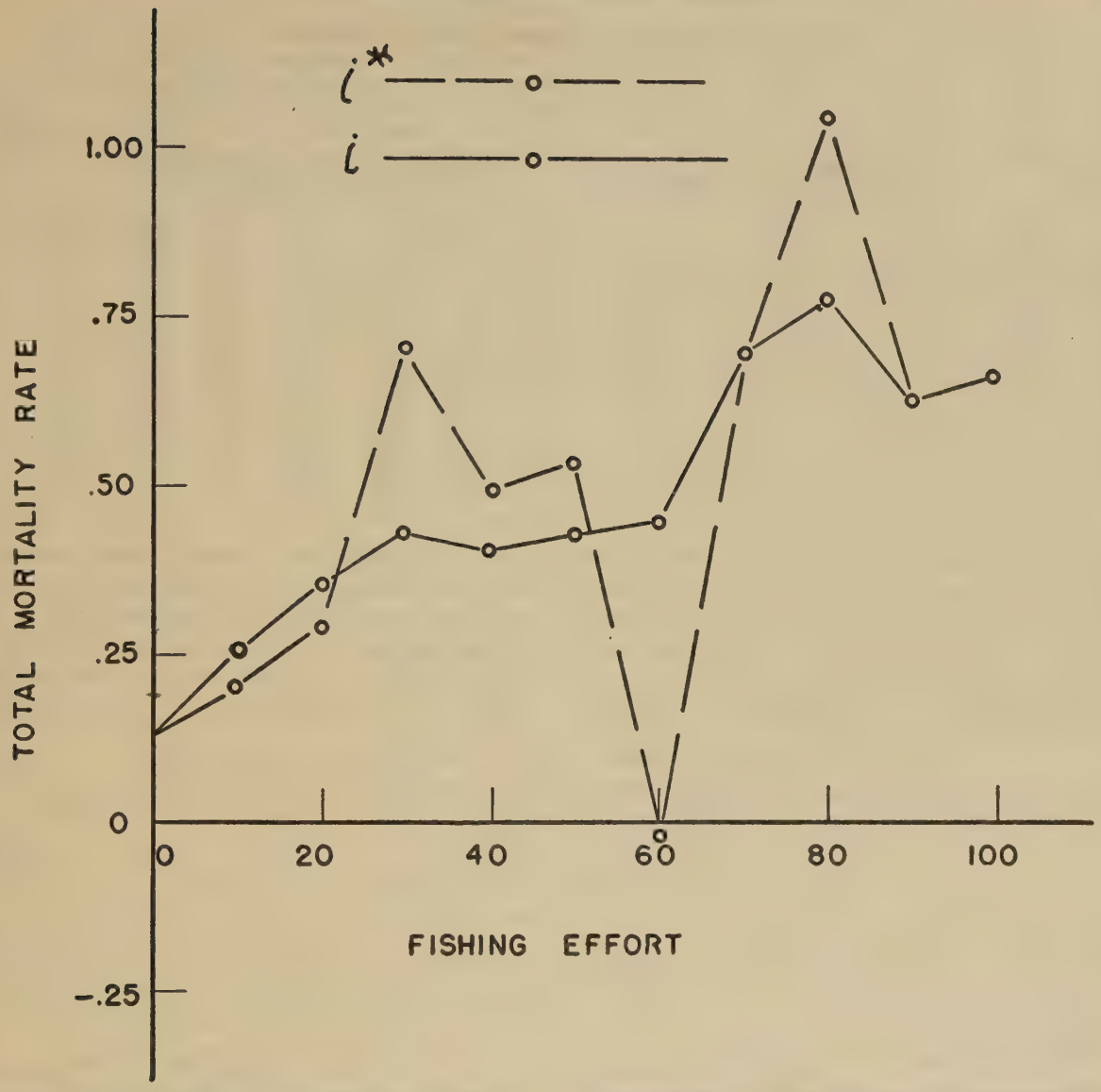

FIGURE 5.—Instantaneous total-mortality rate and fishing effort, with variable level of availability. See text, example 4.

average-population size in the northern area. Therefore, I have averaged the catch per unit-of-effort from these two ports, taking the ratio of the sum of the catches at the two ports to the sum of the efforts at the two ports. The resulting figure should be added, unweighted, to the catch per unit-of-effort at San Pedro to give a catch per unit-of-effort figure for the combined ports that is pertinent to this population study.

Table 6 contains the data necessary to the derivation of the total catch per unit-of-effort figure, which appears in column 11. The total catch is in column 12, and the effective effort for use in a population model is in column 13.

To compute a measure of total mortality, one must know the relative population size of a specific group of fish in at least 2 periods—in this fishery, 2 successive years. A specific group of fish would be an individual year class or a group of year classes. The catch per unit-of-effort of each of the year classes aged as 1 ring (second year of life) through 6 rings, for each of the two areas, and their total, is contained in table 7. The total catch per unit-of-effort for all year classes (column 9, table 7) was separated into that for the individual year classes by reference to the age composition of the sardine catch off

TABLE 6.—*Computation of California catch per unit-of-effort*

(1) Season	Effort			Catch				Catch per unit-of-effort			(12)	(13)
	(2) Monterey	(3) San Francisco	(4) Northern California	(5) Monterey	(6) San Francisco	(7) Northern California	(8) Southern California	(9) Northern California	(10) Southern California	(11) Total California	Total California catch	Total California effective effort
1932–33	205.2	133.4	338.6	496	366	862	509	2,546	2,045	4,591	1,371	299
1933–34	351.3	165.6	516.9	830	490	1,320	790	2,554	2,829	5,383	2,110	392
1934–35	343.0	209.1	552.1	1,345	927	2,272	1,225	4,115	3,239	7,354	3,497	476
1935–36	389.3	277.3	666.6	1,118	1,237	2,355	1,053	3,533	2,441	5,974	3,408	570
1936–37	410.2	518.0	928.2	1,273	2,232	3,505	937	3,776	1,725	5,501	4,442	807
1937–38	447.5	542.0	989.5	725	1,196	1,921	867	1,941	1,276	3,217	2,789	867
1938–39	497.7	620.3	1,118.0	1,513	1,732	3,245	1,437	2,903	1,983	4,886	4,683	958
1939–40	603.6	440.2	1,043.8	1,721	1,544	3,265	863	3,128	1,487	4,615	4,128	894
1940–41	563.8	226.8	790.6	1,424	886	2,310	1,712	2,922	2,350	5,272	4,022	763
1941–42	706.5	294.0	1,000.5	2,378	1,441	3,819	1,524	3,817	1,984	5,801	5,344	921
1942–43	538.7	213.1	751.8	1,337	732	2,069	1,920	2,752	2,622	5,374	3,988	742
1943–44	588.8	234.0	822.8	1,496	717	2,213	1,241	2,690	1,498	4,188	3,453	824
1944–45	701.2	437.0	1,138.2	1,652	692	2,344	1,466	2,059	2,147	4,206	3,810	906
1945–46	733.2	353.7	1,086.9	895	454	1,349	1,444	1,241	1,930	3,171	2,793	881
1946–47	639.1	----------	639.1	187	----------	187	1,688	293	1,269	1,562	1,893	1,212
1947–48	639.9	----------	639.9	131	----------	131	792	205	558	763	927	1,215
1948–49	539.2	----------	539.2	475	----------	475	1,004	880	1,221	2,101	1,493	711
1949–50	461.2	----------	461.2	937	----------	937	1,698	2,055	2,172	4,227	2,757	652
1950–51	774.3	----------	774.3	271	----------	271	2,319	350	1,378	1,728	2,590	1,499

the Pacific coast for the seasons 1941–42 through 1951–52, as given by Felin and Phillips (1948); Mosher, Felin, and Phillips (1949); Felin, Phillips, and Daugherty (1949); Felin, Daugherty, and Pinkas (1950 and 1951); Felin, Anas, Daugherty, and Pinkas (1952). I used the seasons' total "age composition of the catch" from the ports concerned. For the seasons 1932–33 through 1937–38, I used the season's total age composition from the ports of Monterey and San Pedro, as reported by Eckles (1954). Age data for the three seasons, 1938–39, 1939–40, and 1940–41, are not available.

TABLE 7.—*Age composition of California catch per unit-of-effort, 1932–33 to 1950–51*

[The sum of the catch per unit-of-effort in the two separate areas, northern California and southern California]

(1) Season	(2) 0-ring	(3) 1-ring	(4) 2-ring	(5) 3-ring	(6) 4-ring	(7) 5-ring	(8) 6-ring	(9) Total catch per unit-of-effort
1932–33:								
North	----------	----------	187.5	679.0	706.5	424.5	223.2	2,546
South	----------	26.3	141.0	867.5	761.9	176.5	49.2	2,045
Total	----------	26.3	328.5	1,546.5	1,468.4	601.0	272.4	4,591
1933–34:								
North	----------	31.9	439.1	408.8	463.2	426.5	291.5	2,554
South	----------	268.1	472.5	320.3	436.4	499.9	329.4	2,829
Total	----------	300.0	911.6	729.1	899.6	926.4	620.9	5,383
1934–35:								
North	----------	87.7	1,003.1	1,478.9	565.9	334.8	304.7	4,115
South	----------	19.3	800.9	1,015.2	466.5	259.7	280.6	3,239
Total	----------	107.0	1,804.0	2,494.1	1,032.4	594.5	585.3	7,354
1935–36:								
North	----------	66.8	510.1	1,596.8	730.9	229.7	334.6	3,533
South	----------	----------	479.3	1,575.0	276.8	78.0	10.9	2,441
Total	----------	66.8	989.4	3,171.8	1,007.7	307.7	345.5	5,974
1936–37:								
North	----------	28.7	567.2	863.4	1,283.9	675.0	197.8	3,776
South	----------	----------	26.4	361.0	972.0	329.5	19.3	1,725
Total	----------	28.7	593.6	1,224.4	2,255.9	1,004.5	217.1	5,501
1937–38:								
North	2.7	146.2	779.1	365.7	252.6	238.3	68.4	1,941
South	2.2	68.4	488.8	198.0	310.2	162.8	39.6	1,276
Total	4.9	214.6	1,267.9	563.7	562.8	401.1	108.0	3,217
1941–42:								
North	----------	266.1	2,170.6	1,091.5	225.1	52.2	7.0	3,817
South	----------	246.0	1,028.6	607.5	74.7	22.2	4.8	1,984
Total	----------	512.1	3,199.2	1,699.0	299.8	74.4	11.8	5,801

TABLE 7.—*Age composition of California catch per unit-of-effort, 1932-33 to 1950-51*—Continued

[The sum of the catch per unit-of-effort in the two separate areas, northern California and southern California]

(1) Season	(2) 0-ring	(3) 1-ring	(4) 2-ring	(5) 3-ring	(6) 4-ring	(7) 5-ring	(8) 6-ring	(9) Total catch per unit-of-effort
1942–43:								
North		65.5	419.1	1,392.3	633.7	172.4	58.6	2,752
South		320.0	987.7	938.9	320.2	42.5	11.1	2,622
Total		385.5	1,406.8	2,331.2	953.9	214.9	69.7	5,374
1943–44:								
North		338.3	150.0	739.9	1,006.2	338.7	89.7	2,690
South		231.3	559.5	421.8	226.3	47.8	10.4	1,498
Total		569.6	709.5	1,161.7	1,232.5	386.5	100.1	4,188
1944–45:								
North		201.6	686.0	191.7	342.8	421.6	156.3	2,059
South		284.3	676.5	775.6	281.9	104.9	18.4	2,147
Total		485.9	1,362.5	967.3	624.7	526.5	174.7	4,206
1945–46:								
North		50.4	351.3	431.7	191.5	109.1	72.1	1,241
South		252.9	698.6	488.9	359.1	104.5	20.8	1,930
Total		303.3	1,049.9	920.6	550.6	214.6	72.9	3,171
1946–47:								
North	3.4	123.8	39.5	56.1	32.8	18.7	8.6	293
South	.5	519.2	378.6	251.6	87.0	28.3	2.2	1,269
Total	3.9	643.0	418.1	307.7	119.8	47.0	10.8	1,562
1947–48:								
North		102.3	59.1	20.4	11.5	7.9	3.0	205
South	20.0	134.5	193.8	111.1	57.3	31.0	7.6	558
Total	20.0	236.8	252.9	131.5	68.8	38.9	10.6	763
1948–49:								
North	1.3	719.0	125.9	24.1	7.4	2.0	.3	880
South		121.5	832.8	181.4	65.0	18.0	2.4	1,221
Total	1.3	840.5	958.7	205.5	72.4	20.0	2.7	2,101
1949–50:								
North		36.1	1,360.6	430.7	134.7	69.4	16.7	2,055
South		252.2	916.7	699.9	200.4	96.5	5.5	2,172
Total		288.3	2,277.3	1,130.6	335.1	165.9	22.2	4,227
1950–51:								
North			56.9	150.1	113.1	19.1	10.3	350
South			640.5	519.2	178.7	55.1	4.5	1,378
Total			697.4	669.3	291.8	74.2	14.8	1,728

APPLICATION AND RESULTS

The first approximations (using catch per unit-of-effort) to s^* are in column 4 of table 8, using a weighted mean of the survival rate of three year classes in each pair of successive seasons as follows:

$$s^* = \frac{A_4 + B_5 + C_6}{A_3 + B_4 + C_5}$$

where A, B, and C are the catch per unit-of-effort measures of the three year classes. The subscripts refer to the age of each year class. This estimate is a weighted mean—weighted to the catch per unit-of-effort of the year classes as 3-, 4-, and 5-ring fish. This procedure gives more emphasis to the younger fish, whose sample size is usually larger. The variance of these age-composition estimates is usually inversely proportional to their sample size, so the more reliable measures have greater emphasis in this computation.

The correction factors, a/i, are computed from the s' (the survival rates from the regression line), and the corrected s^* is in column 10.

In figure 6, the i^*'s are plotted as ordinates, and California effective effort as abscissae. Clearly, the apparent efficiency, or effectiveness, of a unit-of-effort varies widely. The physical characteristics of the effort have been standardized in the process of computing catch per unit-of-effort (see Clark and Daugherty 1950). Any variation in the total-mortality rate, then, must be ascribed to variation in natural mortality or in availability, or both. I shall describe the variation in the one, holding the other constant, that

TABLE 8.—*Estimation of total-mortality rate from the California catch per unit-of-effort in the available population*

N_2=sum of year class catch per unit of effort for 4-, 5-, and 6-ring fish
N_1=sum of year class catch per unit of effort for 3-, 4-, and 5-ring fish
s_1^*=estimate of $s_1=\frac{N_2}{N_1}$
i^*=estimate of $i=-\log_e s^*$
f=fishing effort
i'=estimated i from regression of i^* on f
$(i'/a)=(i'/1-e^{-i'})$
Ratio=ratio of (i/a): $\frac{(i/a)_2'}{(i/a)_1'}$
$s^{**}=s^*$ corrected for changing fishing effort—after the first iteration

(1) Season	(2) N_2	(3) N_1	(4) s^*	(5) i^*	(6) f	(7) i'	(8) (i'/a)	(9) Ratio	(10) s^{**}
1932–33		3,615.9	0.677	0.390	299	0.343	1.183	1.046	0.708
1933–34	2,446.9	2,555.1	.866	.147	392	.439	1.237	1.042	.902
1934–35	2,212.2	4,121.0	.403	.910	476	.527	1.289	1.043	.420
1935–36	1,660.9	4,487.2	.775	.252	570	.624	1.345	1.113	.863
1936–37	3,477.5	4,484.8	.239	1.430	807	.870	1.497	1.029	.246
1937–38	1,071.9				867	.933	1.540		
1938–39					958	1.027			
1939–40					894	.961			
1940–41					763	.825			
1941–42		2,073.2	.597	.514	921	.989	1.577	.924	.552
1942–43	1,238.5	3,500.0	.491	.711	742	.803	1.457	1.036	.509
1943–44	1,719.1	2,780.7	.477	.740	824	.888	1.510	1.034	.493
1944–45	1,325.9	2,118.5	.396	.923	906	.973	1.562	.990	.392
1945–46	839.1	1,685.8	.105	2.250	881	.947	1.547	1.151	.121
1946–47	177.6	474.5	.249	1.390	1,212	1.291	1.781	1.002	.249
1947–48	118.3	239.2	.398	.922	1,215	1.294	1.785	.803	.320
1948–49	95.1	297.9	1.756	−.563	711	.771	1.433	.974	1.710
1949–50	523.2	1,631.6	.233	1.453	652	.709	1.396	1.431	.333
1950–51	380.8				1,499	1.590	1.997		

is necessary to produce the observed variation in estimated total-mortality rate. The corresponding population estimates will then be possibilities, rather than estimates with known probability of accuracy. The selection of any given set can only be based on an individual's judgment of which conditions most nearly describe the true history of the population as regards its availability and natural mortality.

Population Size Assuming Constant Availability

If the entire population is available to the effort of the fishing fleet, then any variation in total-mortality rate, for given level of effort, must be due to variation in the rate of natural mortality. Or if the level of availability is assumed constant, variation in total-mortality rate must again be interpreted as due only to variation in natural-mortality rate. If one assumes full availability, then the relation of instantaneous fishing mortality, p, to fishing effort, f, is one of direct proportion:

$$p=Qf$$

If availability is assumed constant, at some given level, say r_o, then the relation of instantaneous fishing mortality to fishing effort is nearly proportional—p being a little less than directly proportional to f as f increases:

$$p=-\log_e [r_o e^{-Q_a f}+(1-r_o)]$$

In either case, the difference between the total-mortality rate, i, and the fishing-mortality rate, p, must be interpreted as the rate of natural mortality, q. And in either case, variation in i, for given f (with r assumed full or constant), implies variation in q.

Table 9 contains the minimum natural-mortality rates, under the hypothesis of full, or 100 percent, availability (column 5). These rates are minimal because the season of lowest relative natural mortality, 1935–36, was taken as zero natural mortality, and it could be no less. The corresponding total-population estimates (column 9) are therefore also minimal. The seasonal, or percentage, natural-mortality rate, if there were no fishing, n, corresponding to q, is contained in column 10. Since the estimated total-mortality rate for the season 1948–49 is negative, there must have been a change in availability between the seasons 1948–49 and 1949–50—the availability level in the later season being higher than in the earlier. Under the hypothesis of no change in availability, then, the season 1948–49 must be omitted.

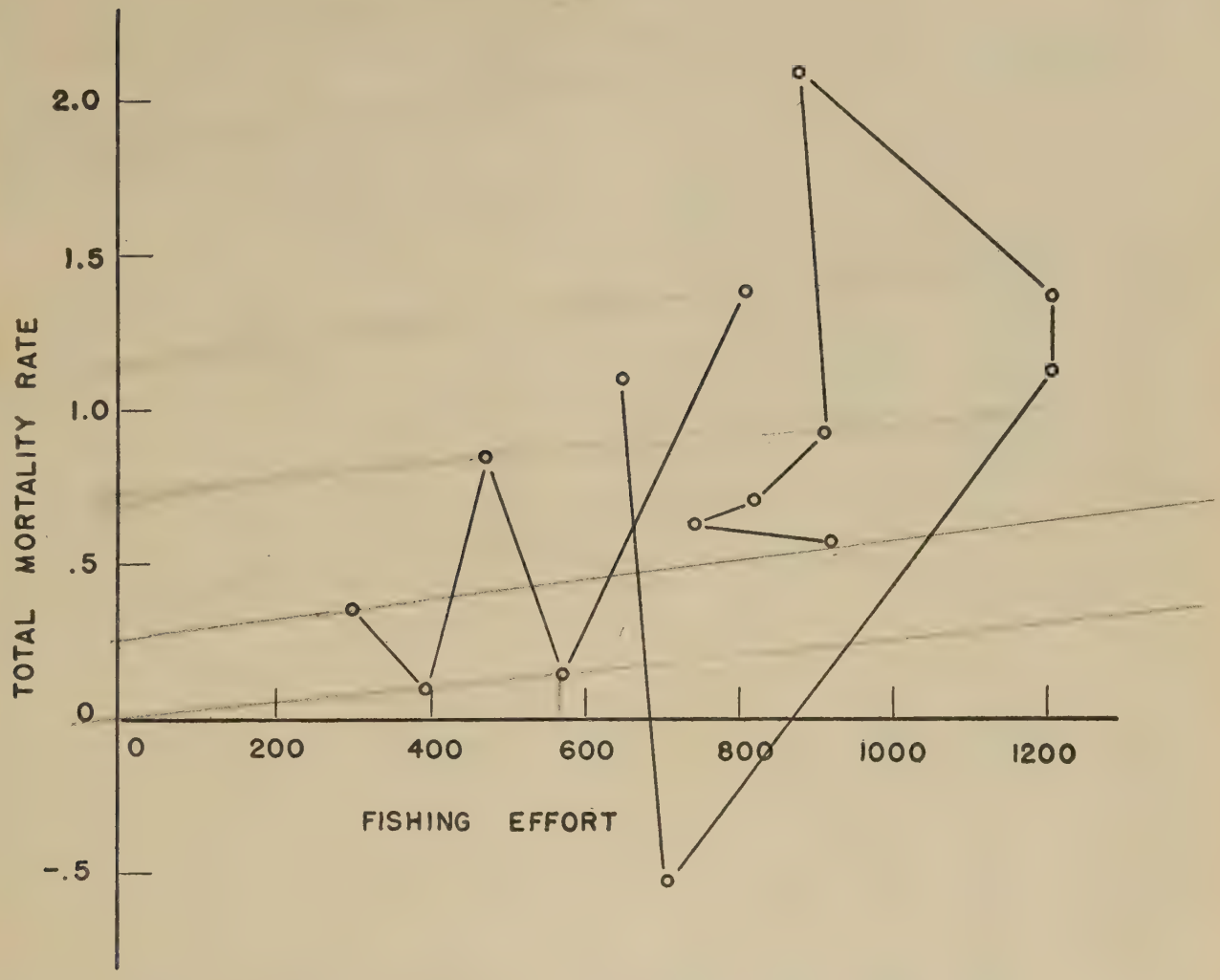

FIGURE 6.—California fishing effort and the apparent instantaneous total-mortality rate.

If the availability level is taken as constant, but less than 100 percent, the necessary natural mortality to produce the observed estimated total-mortality rate can easily be computed, for any given level of availability. Table 10 contains the necessary natural-mortality rates, under the hypothesis of constant availability at 50 percent. Table 11 contains the corresponding population sizes: the available population, N_a, in column 9, and the total-population size, N, in column 10. Again, natural mortality was assumed zero in the year of relative minimum natural mortality, 1935–36. The only major difference in the two situations—full availability or not—is that with less than full availability, the exploitation rate, u, is necessarily greater. The resulting natural-mortality rates, even under two such different conditions of constant availability, are nearly the same. The population sizes resulting from the two situations are also nearly the same.

The possibility of some or all of the variation in total-mortality rate being due simply to variation in the availability level can be explored. Between 1948 and 1949 some change in availability must have taken place. A change from high availability to low would result in an apparent abnormally high total-mortality rate. So an increase in total-mortality rate as computed here could result either from an increase in natural-mortality rate or from a decrease in the availability level between the two seasons from which the total-mortality rate was computed. Without an independent measure of the natural-mortality rate, and without a direct estimate of the avail-

TABLE 9.—*Estimated minimum-population size of fish, 2 rings and older, under the hypothesis of full availability, 1932–33 to 1950–51*

(1) Season	(2) f	(3) Qf	(4) i	(5) Minimum q	(6) a	(7) u	(8) C	(9) N	(10) n
							Billions	*Billions*	*Percent*
1932–33	299	0.077	0.345	0.268	0.292	0.065	1.3	20.0	23
1933–34	392	.101	.103	.002	.098	.096	2.0	20.8	0
1934–35	476	.123	.868	.745	.580	.082	3.5	42.7	53
1935–36	570	.147	.147	0	.137	.137	3.4	24.8	0
1936–37	807	.208	1.407	1.199	.754	.112	4.4	39.3	70
1937–38	867	.224							
1938–39	958	.247							
1939–40	894	.231							
1940–41	763	.197							
1941–42	921	.238	.595	.356	.448	.180	4.8	26.7	30
1942–43	742	.191	.675	.484	.491	.139	3.7	26.6	38
1943–44	824	.213	.707	.494	.507	.153	3.0	19.6	39
1944–45	906	.234	.936	.702	.608	.152	3.4	22.4	50
1945–46	881	.227	2.112	1.885	.879	.094	2.6	27.7	85
1946–47	1,212	.313	1.390	1.077	.751	.169	1.1	6.5	66
1947–48	1,215	.313	1.139	.826	.680	.187	.6	3.2	56
1948–49	711	.183					1.0		"0"
1949–50	652	.168	1.100	.932	.667	.102	2.5	24.5	61
1950–51	1,499	.387					2.6		

TABLE 10.—*Computation natural-mortality rate under the hypothesis of constant availability at 50 percent, 1932–33 to 1950–51*

(1) Season	(2) f	(3) p	(4) i	(5) Minimum q	(6) n
					Percent
1932–33	299	0.081	0.345	0.264	23
1933–34	392	.099	.103	.004	0
1934–35	476	.124	.868	.744	52
1935–36	570	.147	.147	0	0
1936–37	807	.201	1.407	1.206	70
1937–38	867	.214			
1938–39	958	.233			
1939–40	894	.221			
1940–41	763	.191			
1941–42	921	.226	.595	.369	31
1942–43	742	.188	.675	.487	39
1943–44	824	.206	.707	.501	39
1944–45	906	.223	.936	.713	51
1945–46	881	.217	2.112	1.895	85
1946–47	1,212	.284	1.390	1.106	67
1947–48	1,215	.284	1.139	.855	57
1948–49	711	.180			"0"
1949–50	652	.167	1.100	.933	61
1950–51	1,499	.335			

TABLE 11.—*Estimated minimum-population size of fish 2 rings and older, under the hypothesis of constant availability at 50 percent, 1932–33 to 1949–50*

(1) Season	(2) f	(3) p_a	(4) Minimum q	(5) i_a	(6) a_a	(7) u_a	(8) C	(9) N_a	(10) N
							Billions	*Billions*	*Billions*
1932–33	299	0.168	0.264	0.432	0.351	0.137	1.3	9.5	19.0
1933–34	392	.220	.004	.224	.201	.197	2.0	10.2	20.4
1934–35	476	.267	.744	1.011	.636	.168	3.5	20.8	41.6
1935–36	570	.320	0	.320	.274	.274	3.4	12.4	24.8
1936–37	807	.453	1.206	1.659	.810	.221	4.4	19.9	39.8
1937–38	867	.487							
1938–39	958	.538							
1939–40	894	.502							
1940–41	763	.428							
1941–42	921	.517	.369	.886	.588	.343	4.8	14.0	28.0
1942–43	742	.417	.487	.904	.595	.274	3.7	13.5	27.0
1943–44	824	.463	.501	.964	.619	.297	3.0	10.1	20.2
1944–45	906	.509	.713	1.222	.705	.294	3.4	11.6	23.2
1945–46	881	.495	1.895	1.390	.751	.267	2.6	9.7	19.4
1946–47	1,212	.680	1.106	1.786	.832	.317	1.1	3.5	7.0
1947–48	1,215	.682	.855	1.537	.785	.348	.6	1.7	3.4
1948–49	711	.399					1.0		
1949–50	652	.366	.933	1.299	.727	.205	2.5	12.2	24.4
1950–51	1,499	.842					2.6		

ability change, one must ascribe the variation in total-mortality rate to a change in either or both of these factors.

Having described the necessary change in natural mortality under the hypothesis of constant availability, I shall now consider the necessary changes in availability level, under the hypothesis of constant natural mortality.

Population Size Assuming Constant Natural-Mortality Rate

I would expect the distribution of a fish population, relative to a fishery, to change more readily than the natural mortality in that population. Having no really direct evidence of the level or variability of natural mortality, one must keep its possible influence in mind in interpreting computed availability measures. For example, I would place more significance in an estimated large change in availability than in a small one, when natural mortality was assumed constant. This is, of course, a subjective qualification—an opinion—and not evidence.

Since the rate of natural mortality is unknown, I have computed several sets of availability measures, each based on a different but possible constant rate of natural mortality. Generally, the higher the true average rate of natural mortality, the less variable are the computed availability measures. That is, the possible range of percentage variation in i to be expected from a given change in availability is less, the higher the level of natural mortality assumed. The reason for this, intuitively, is that natural mortality takes place in both the available and unavailable population, and the higher it is, the less will be the effect of the fishing mortality on the total-mortality rate, regardless of the level of availability.

The following computations will rest on the assumption that natural mortality is constant. The procedure has been outlined in previous sections.

First estimates of the ratio of the availability level between successive pairs of years for three assumed constant natural-mortality rates are in columns 5, 8, and 11 of table 12. Taking these ratios, a series of maximum-availability levels is in columns 6, 9, and 12. These are maximal, since it is necessary, of course, to assume that in some one year the entire population is available. In these data, there are two periods where this assumption

TABLE 12.—*Estimation of availability level, for various assumed rates of natural mortality and corresponding estimated total mortality in the total population*

For $\begin{cases} q=0,\ Q=.001036 \\ q=0.2,\ Q=.000772 \\ q=0.4,\ Q=.000508 \end{cases}$

$s^*=s^{**}$ from previous tables
f=fishing effort
$s'=e^{Qf-q}$
s'/s^*=estimate of (r_1/r_2)
r^*=maximum estimate of the availability level, r

(1)	(2)	(3)	$q=0$			$q=0.2$			$q=0.4$		
Season	s^*	f	(4) s'	(5) s'/s^*	(6) r^*	(7) s'	(8) s'/s^*	(9) r^*	(10) s'	(11) s'/s^*	(12) r^*
1932–33	0.708	299	0.734	1.037	71.4	0.650	0.918	50.9	0.576	0.814	36.1
1933–34	.902	392	.666	.738	68.9	.605	.671	55.4	.549	.609	44.4
1934–35	.420	476	.611	1.455	93.3	.567	1.350	82.5	.526	1.252	72.9
1935–36	.863	570	.553	.641	64.1	.527	.611	61.1	.502	.582	58.2
1936–37	.246	807	.434	1.764	100.0	.439	1.785	100.0	.445	1.809	100.0
1937–38		867			53.6	.419		56.0	.432		55.3
1938–39		958				.391			.412		
1939–40		894				.411			.426		
1940–41		763				.454			.455		
1941–42	.552	921	.385	.697	51.4	.402	.728	58.0	.420	.761	61.6
1942–43	.509	742	.463	.910	73.8	.462	.908	79.7	.460	.904	80.9
1943–44	.493	824	.425	.862	81.1	.433	.878	87.8	.441	.895	89.5
1944–45	.392	906	.391	.997	94.1	.407	1.038	100.0	.423	1.079	100.0
1945–46	.121	881	.401	3.314	94.4	.415	3.430	96.3	.428	3.537	92.7
1946–47	.249	1,212	.285	1.145	28.5	.321	1.289	28.1	.362	1.454	26.2
1947–48	.320	1,215	.284	.888	24.9	.320	1.000	21.8	.362	1.131	18.0
1948–49	1.710	711	.479	.280	28.0	.473	.277	21.8	.467	.273	15.9
1949–50	.333	652	.509	1.529	100.0	.495	1.486	78.7	.481	1.444	58.2
1950–51		1,499			65.4	.257		53.0	.313		40.3
			$\bar{r}=68.3$			$\bar{r}=64.4$			$\bar{r}=59.4$		

is necessary, since the series is broken from 1937–38 to 1941–42.

Now the value of Q_a can be computed by

$$Q_a=\frac{\log_e\left[\dfrac{\bar{s}-\bar{s}_u(1-\bar{r})}{\bar{r}\,\bar{s}_u}\right]}{\bar{f}}$$

I have assumed several different possible values for $\bar{q}$ and shall compute the stock-size series for each as being possible. If $\bar{q}$ be taken as 0.2, and with $\bar{i}=.785$ and $\bar{f}=758$, and $\bar{r}=65$ percent, Q_a takes the value 0.00151. Computation of Q_a for the three levels of natural mortality are in table 13. The computation, from previous sections, of the adjusted r, is in table 14, and the computation of the available and total stock-size series is in table 15. These total-stock-size estimates are minimums, but have considerable possible variance, since the estimates of availability are not precise. They simply suggest the general order of the stock size in the past, under the hypothesis of constant natural mortality.

TABLE 13.—*Computation of* Q_a *for various assumed natural-mortality rates* (q), *and the corresponding average fishing effort, average total-mortality rate, and average maximum estimate-of-availability level*

Constants $\begin{cases} \bar{f}=758 \\ \bar{i}^*=.785,\ \bar{s}^*=.456 \end{cases}$

$\bar{r}^*$=estimate of $\bar{r}$, from previous tables

Q_a^*=estimated constant fishing effort unit efficiency $=\dfrac{-\log_e\left[\dfrac{\bar{s}^*-(1-\bar{r}^*)s_u}{\bar{r}^*\,s_u}\right]}{\bar{f}}$

	$q=0$	q=0.2	q=0.4
Q^*	0.001036	0.000772	0.000508
$\bar{r}^*$	.683	.644	.594
Q_a^*	.002098	.001533	.001018
s_u	1.000	.8187	.6703

SUMMARY

Estimates of the total-population survival rate were computed from data on the age composition of the commercial catch of Pacific sardines in California and from the catch per unit-of-effort of the fleet, for the period 1932–33 through 1950–51.

TABLE 14.—*Estimation of availability level, from availability-corrected estimates of survival rate, corresponding to various assumed natural-mortality rates*

$$s' = e^{-q+\log_e [r(1-e^{-Q_a f})-1]}$$

(1) Season	$q=0$			$q=0.2$			$q=0.4$		
	(2) s'	(3) s'/s^*	(4) Maximum r	(5) s'	(6) s'/s^*	(7) Maximum r	(8) s'	(9) s'/s^*	(10) Maximum r
1932–33	0.682	0.963	53.9	0.624	0.881	43.6	0.566	0.799	33.9
1933–34	.618	.685	56.0	.580	.643	49.5	.540	.599	42.4
1934–35	.567	1.350	81.8	.545	1.298	77.0	.517	1.231	70.8
1935–36	.523	.606	60.6	.512	.593	59.3	.496	.575	57.5
1936–37	.443	1.801	100.0	.444	1.805	100.0	.447	1.817	100.0
1937–38	.428		55.5	.431		55.4	.437		55.0
1938–39	.409			.413			.422		
1939–40	.421			.426			.432		
1940–41	.455			.455			.455		
1941–42	.416	.754	60.8	.420	.761	61.5	.428	.775	63.0
1942–43	.461	.906	80.6	.461	.906	80.8	.459	.902	81.3
1943–44	.439	.890	89.0	.440	.892	89.2	.444	.901	90.1
1944–45	.419	1.069	100.0	.422	1.077	100.0	.430	1.097	100.0
1945–46	.425	3.512	93.5	.428	3.537	92.9	.434	3.587	91.2
1946–47	.370	1.486	26.6	.373	1.498	26.3	.388	1.558	25.4
1947–48	.370	1.156	17.9	.373	1.166	17.6	.387	1.209	16.3
1948–49	.471	.275	15.5	.468	.274	15.1	.465	.272	13.5
1949–50	.491	1.474	56.4	.485	1.456	55.1	.477	1.432	49.6
1950–51	.346		38.3	.344		37.8	.359		34.6
			$\bar{r}=61.7$			$\bar{r}=60.1$			$\bar{r}=57.8$

TABLE 15.—*Minimal estimates of population size, available and total, for various assumed rates of natural mortality*

C=California catch in billions of fish 2 rings and older

u_a=estimated rate of exploitation in available population=$Q_a f\left(\frac{a}{i}\right)_a$

N_a=California available population size in billions of fish

N=minimal estimate of total population in billions of fish

(1) Season	(2) C	$q=0$				$q=0.2$				$q=0.4$			
		(3) u_a	(4) N_a	(5) Maximum r	(6) Minimum N	(7) u_a	(8) N_a	(9) Maximum r	(10) Minimum N	(11) u_a	(12) N_a	(13) Maximum r	(14) Minimum N
1932–33	1.3	0.465	2.8	53.9	5.2	0.336	3.9	43.6	8.9	.219	5.9	33.9	17.4
1933–34	2.0	.560	3.6	56.0	6.4	.413	4.8	49.5	9.7	.275	7.3	42.4	17.2
1934–35	3.5	.632	5.5	81.8	6.7	.475	7.4	77.0	9.6	.321	10.9	70.8	15.4
1935–36	3.4	.698	4.9	60.6	8.1	.536	6.3	59.3	10.6	.369	9.2	57.5	16.0
1936–37	4.4	.816	5.4	100.0	5.4	.656	6.7	100.0	6.7	.478	9.2	100.0	9.2
1937–38	2.6	.838	3.1	55.5	5.6	.680	3.8	55.4	6.9	.498	5.2	55.0	9.5
1938–39		.866				.714				.529			
1939–40		.847				.691				.507			
1940–41		.798				.636				.456			
1941–42	4.8	.855	5.6	60.8	9.2	.702	6.8	61.5	11.1	.518	9.3	63.0	14.8
1942–43	3.7	.789	4.7	80.6	5.8	.628	5.9	80.8	7.3	.448	8.3	81.3	10.2
1943–44	3.0	.822	3.6	89.0	4.0	.633	4.5	89.2	5.0	.481	6.2	90.1	6.9
1944–45	3.4	.850	4.0	100.0	4.0	.696	4.9	100.0	4.9	.512	6.6	100.0	6.6
1945–46	2.6	.842	3.1	93.5	3.3	.686	3.8	92.9	4.1	.501	5.2	91.2	5.7
1946–47	1.1	.922	1.2	26.6	4.5	.788	1.4	26.3	5.3	.608	1.8	25.4	7.1
1947–48	.6	.922	.7	17.9	3.9	.788	.8	17.6	4.5	.609	1.0	16.3	6.1
1948–49	1.0	.775	1.3	15.5	8.4	.613	1.6	15.1	10.6	.435	2.3	13.5	17.0
1949–50	2.5	.745	3.4	56.4	6.0	.582	4.3	55.1	7.8	.409	6.1	49.6	12.3
1950–51	2.6	.957	2.7	38.3	7.0	.843	3.1	37.8	8.2	.676	3.8	34.6	11.0
1951–52	.9												

The total-population size for each year was estimated from the survival-rate data, under the hypothesis of constant availability level. Variation in estimated-survival rate for a given level of fishing effort was therefore ascribed to the necessary change in natural mortality. The population-size estimates are nearly the same for either the assumed full level of availability, or for the assumed 50-percent level of availability.

The total-population size for each year was also estimated from the survival-rate data under the hypothesis of constant natural-mortality rate. Variation in estimated-survival rate for a given level of fishing effort was therefore ascribed to the necessary change in the level of availability between successive seasons. The computation was carried through for each of several possible rates of natural mortality.

NOTATION

Population numbers:
- N_____ initial population.
- C_____ catch.
- D_____ deaths from all causes.

Annual mortality rates:
- u_____ catch fraction (rate of exploitation).
- v_____ natural death fraction.
- a_____ total mortality fraction.
- s_____ total survival fraction.
- m_____ fishing mortality (in absence of natural mortality).
- n_____ natural mortality (in absence of fishing).

Instantaneous mortality rates:
- p_____ fishing.
- q_____ natural.
- i_____ total.
- f_____ effective fishing effort.

Miscellaneous:
- Q_____ fishing effort efficiency, or constant of proportionality between p and f.
- r_____ availability fraction.

Subscripts:
- a_____ available population (in fished area).
- u_____ unavailable population (in unfished area).
- t_____ total population.

Superscripts:
- $*$_____ a statistic: Estimate of a parameter.
- $'$_____ a statistic: Estimate of a parameter.

APPENDIX

USING CATCH PER UNIT-OF-EFFORT TO MEASURE POPULATION SIZE

Let a unit-of-effort be the operation of a unit of fishing gear (net, hook, or trap) for a certain period of time (hour, day, or month). If the gear chosen is standard (constant), then the area of the fish's habitat that the unit of gear fishes (or scouts) in a fixed interval of time should be a constant area. Further, if the gear strains or otherwise attracts fish to it, and catches fish if they are within this area, let us describe this catching power quantitatively by noting that, for most gear, the more fish in the area, the greater will be the catch, and the fewer fish in the area, the smaller the catch. However, if fish are extremely numerous, as they may be, let us admit that the gear may become filled with fish and stop being effective in catching more. If the time during which the gear is thus not fishing is recognized, that time could be deducted from the total fishing time and saturation would not affect the reliability of the reported catching time. Some gear, such as longlines and gill nets, may vary in effectiveness with varying densities of fish in the area fished.

To be entirely general, let us say that a unit-of-effort becomes fully saturated when the catch is some contant, say C_s. When the gear contains no fish, but is being fished, let us say the gear is capable of taking some constant fraction of the fish in the area that is being fished—that is, some fraction of the population in an area fished is caught, and the remainder is not caught. Let the ratio of those caught, to the total before fishing took place, be E. This fraction might be termed the efficiency of fishing. Now as the gear becomes filled with fish, let us say (a) the efficiency of the gear stays constant, or (b) it decreases, in direct proportion as the ratio of catch to the saturated catch.

If n is the population in the fished area during a very short period of time, dt, let the rate of catch be:

$$\frac{dC}{dt}=En \tag{1}$$

for the fished area, say α, in time dt. Note that the catch, dC, is directly proportional to the number of fish in the area α. From this it follows that the instantaneous density of catch, $\frac{dC}{\alpha}$, is directly proportional to the density of fish in the area, $\frac{n}{\alpha}$, and that the constant of proportionality is E. These relations form the basis of using fishery statistics to estimate fish-population size.

Estimation

If a unit-of-effort operates within an area larger than α, and wherein density of fish is uniform

(equal), then the catch of that unit-of-effort constitutes a sample—usually a random one—of the density of fish in that larger area. If we denote by A the large area within which density is uniform, and by N the population size in that area, then:

$$\frac{N}{A}=\frac{n}{\alpha}$$

$$=\frac{dC}{\alpha}\left(\frac{1}{E}\right)$$

So, if α and E are constant, then the instantaneous catch (per unit-of-effort) is directly proportional to the standing population density. Of course, if the area A is known, the product of dC and A gives a measure of the relative size of the population that is sampled in the area A:

$$N=dC\left[\left(\frac{1}{\alpha E}\right)A\right]$$

where $\left[\left(\frac{1}{\alpha E}\right)A\right]$ is the constant of direct proportionality.

Now fishery data yield not measures of dC, but of its integral, over some finite period of time, such as a day, a week, or a year.

Taking some unit of time as a standard unit that can be reported upon, the catch over that unit of time, say C, is often easily determined for a fishery.

Now if several, say f, units of fishing effort are operating in the area A at the same time, then in the instant dt they are all fishing the same population density, or size, in that area, if each unit's efficiency is the same. This may be written

$$\frac{dC}{dt}=f(En)$$

where each unit's E and α are equal.

Since

$$\frac{n}{\alpha}=\frac{N}{A}$$

$$n=\frac{\alpha}{A}N$$

so

$$\frac{dC}{dt}=f\,E\,\frac{\alpha}{A}N$$

Let us write Q for the constant of proportionality of each unit of effort to its instantaneous catch and the standing population size. That is, let

$$Q=E\left(\frac{\alpha}{A}\right)$$

We then have

$$\frac{dC}{dt}=(Qf)N$$

Following Ricker's (1944) notation, we may observe that the proportion of N that is caught, instantaneously, by a given number of effort units, has been called p, in

$$\frac{dC}{dt}=pN$$

Here, then, $p=Qf$, and Q is taken to be constant. It is easy to show that if other causes of death, termed natural, by q, are equal for any fish in the population in an instant, then the total deaths, D, occurring instantaneously are

$$\frac{dD}{dt}=(p+q)N$$

$$=(i)N$$

where

$$i=p+q$$

Whereupon

$$C=p\,\frac{a}{i}\,N_o$$

where N_o is the population size at the beginning of the period during which C is accumulated, and a is $(1-e^{-i})$.

Further,

$$C=p\bar{N}$$

where $\bar{N}$ is the average population during the period of time that C is accumulated, if p and q are constant.

Recall that

$$p=Qf,$$

so

$$C=Qf\bar{N}$$

or

$$\frac{C}{f}=Q\bar{N} \qquad (2)$$

or

$$\frac{C}{f}=QN_o\left(\frac{a}{i}\right) \qquad (3)$$

In equation 2 the catch per unit-of-effort is directly proportional to the average population during the period, while application of the factor $\left(\frac{a}{i}\right)$ gives equation 3, which states how catch per unit-of-effort can be directly proportional to the initial population of the time period.

Note that here Q is constant and does not vary even if f changes; however, if f changes from one period to another, the factor (a/i) will change, although a lesser percentage amount. To summarize, if f changes from one period to another, C/f is directly proportional to $\overline{N}$, while C/f is nearly proportional to N_o and is directly proportional to it if C/f be multiplied by $\left(\frac{i}{a}\right)$.

Of course, if Q is known, C/f can be made to measure the true population size. It is a major problem of population-dynamics studies to determine the value of Q. Now consider the alternative to situation (1) in the opening section:

$$\frac{dC}{dt}=E\left[\frac{C_s-C}{C_s}\right]n \tag{4}$$

Ordinarily, fishing gear will be operated such that the factor $\left[\frac{C_s-C}{C_s}\right]$ is close to unity. With such gear as trawls, it would probably always be unity, but with gear such as longlines or gill nets, it would probably vary directly with the abundance of fish (fish density). Generally such gear is emptied as often as necessary to maintain its maximum efficiency—that is, to keep $\left[\frac{C_s-C}{C_s}\right]$ very close to unity.

If $\left[\frac{C_s-C}{C_s}\right]$ is maintained merely constant, on the average, one may regard, say, E' as simply the product of $\left[\frac{C_s-C}{C_s}\right]$ and E, and consider E' as constant, just as E is considered constant. Then the results for equation 1 are the same as for equation 4.

LITERATURE CITED

Baranov, T. I.
1918. On the question of the biological basis of fisheries. Nauchnyi issledovatelskii institut, Izvestia I (1), pp. 81–128, 12 figs.

Beverton, R. J. H., and S. J. Holt.
In press. The dynamics of fish populations. Fishery Investigations, United Kingdom Ministry Agriculture and Fisheries, London.

Clark, F. N., and A. E. Daugherty.
1950. Average lunar month catch by California sardine fishermen, 1932–33 through 1948–49. California Division Fish and Game, Fish Bulletin No. 76, 28 pp., 6 figs.
1952. Average lunar month catch by California sardine fishermen, 1949–50 and 1950–51. California Fish and Game, vol. 38, No. 1, pp. 85–97, 2 figs.

DeLury, D. B.
1947. On the estimation of biological populations. Biometrics, vol. 3, No. 4, pp. 145–167, 7 figs.

Eckles, Howard H.
1954. Age composition of the commercial catch of Pacific sardines, 1932–38. *In* Age determination of Pacific sardines from otoliths, Research Report 37, United States Fish and Wildlife Service, Washington, D. C.

Felin, F. E., A. E. Daugherty, and Leo Pinkas.
1950. Age and length composition of the sardine catch off the Pacific coast of the United States and Canada in 1949–50. California Fish and Game, vol. 36, No. 3, pp. 241–249, 1 fig.
1951. Age and length composition of the sardine catch off the Pacific coast of the United States and Canada in 1950–51. California Fish and Game, vol. 37, No. 3, pp. 339–349, 1 fig.

Felin, F. E., and J. B. Phillips.
1948. Age and length composition of the sardine catch off the Pacific coast of the United States and Canada, 1941–42 through 1946–47, California Division Fish and Game, Fish Bulletin No. 69, 122 pp., 1 fig.

Felin, F. E., J. B. Phillips, and A. E. Daugherty.
1949. Age and length composition of the sardine catch off the Pacific coast of the United States and Canada in 1948–49. California Fish and Game, vol. 35, No. 3, pp. 165–183, 1 fig.

Felin, F. E., Ray Anas, A. E. Daugherty, and Leo Pinkas.
1952. Age and length composition of the sardine catch off the Pacific coast of the United States in 1951-52. California Fish and Game, vol. 38, No. 3, pp. 427–435.

Marr, J. C.
1951. On the use of terms *abundance, availability* and *apparent abundance* in fishery biology. Copeia, 1951, No. 2, pp. 163–169.

Mosher, K. H., F. E. Felin, and J. B. Phillips.
1949. Age and length composition of the sardine catch off the Pacific coast of the United States and Canada in 1947–48. California Fish and Game, vol. 35, No. 1, pp. 15–40, 1 fig.

RICKER, W. E.

1940. Relation of "catch per unit effort" to abundance and rate of exploitation. Jour. Fisheries Research Board Canada, vol. 5, No. 1, pp. 43–70, 3 figs.

1944. Further notes on fishing mortality and effort. Copeia, 1944, No. 1, pp. 23–44, 1 fig.

1948. Methods of estimating vital statistics of fish populations. Indiana University Publications. Science Series No. 15, 101 pp., 13 figs.

SCHAEFER, M. B.

1951. Estimation of size of animal populations by marking experiments. United States Fish and Wildlife Service, Fishery Bulletin 69, vol. 52, pp. 191–203, 1 fig.

SETTE, O. E.

1950. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part II–Migrations and habits. United States Fish and Wildlife Service, Fishery Bulletin 49, vol. 51, pp. 251–358, 21 figs.

SILLIMAN, R. P.

1943. Studies on the Pacific pilchard or sardine (*Sardinops caerulea*) 5.—A method of computing mortalities and replacements. United States Fish and Wildlife Service, Special Scientific Report No. 24, 10 pp., 2 figs.